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Determining the Utility of Adolescent Live Weight Data to Predict Two-Year-Old Live Weight in New Zealand Dairy Cattle

A thesis presented in partial fulfilment of the requirements for the degree of Master of Science

Master of Science
in
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1. Main Abstract

The purpose of this research was to establish the utility of adolescent live weight data measured across cohorts of growing animals for predicting live weight in first lactation. Live weight is associated with the growth and maintenance feed requirements of a cow. Selection that simultaneously takes account of milk income and feed requirements of dairy cattle can increase future farm profitability. Estimated breeding values (EBVs) for mature cow live weight are currently predicted using Live weight phenotypes measured during lactation. Breeding companies in NZ actively measure the first lactation live weight of a small proportion of the nation's dairy cows—the daughters of their bulls—to improve their ability to identify superior bulls. Accurate EBVs obtained at an earlier age can allow reliable selection of superior young bulls which would shorten the generation interval, increasing the rate of genetic progress. The purpose of this research was to determine the utility of adolescent live weight (i.e. live weight prior to first lactation) for predicting variation in live weight measured in first lactation. We completed two studies. In the first study (Section 4), we produced the (co)variance parameters for live weights measured at four ages, from six months old through to first lactation. Our hypothesis for this study was that live weight measured through adolescence would share a strong positive genetic relationship with live weight measured during lactation. Our results support this hypothesis, as estimates of genetic correlations between weights at different ages ranged from 0.79 to 0.97. In the second study (Section 5), we produced live weight EBVs using live weight measured though adolescence. For comparison, we produced EBVs using just live weight measured during first lactation. Our hypothesis was that the accuracy of the live weight EBVs would be improved by including adolescent live weight. Our results showed that including adolescent live weight phenotypes improved the accuracy of the live weight EBVs for animals with adolescent live weights, and their progeny. We concluded that adolescent live weights are a useful predictor of live weight later in life, and should be incorporated as a predictor trait for the national live weight EBV in NZ.

2. Acknowledgements

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3. Main Introduction

3.1. The New Zealand Dairy Industry

The New Zealand (NZ) dairy industry is predominantly pasture based, and therefore farm management practices are largely dictated by pasture availability. Approximately 30% of operating expenditure on dairy farms is comprised of feed costs (DairyNZ, 2018b), and so maximising feed efficiency is a priority for most farmers. Feed efficiency can be improved through genetic selection and careful management of pastures and animals. Most herds calve annually in spring, to align peak feed requirements with pasture growth. Females are often reared and managed in the same cohort from birth to death. Artificial insemination (AI) is widely used, such that sires are usually represented across many contemporary groups. These large contemporary groups that can persists for many years, coupled with the widespread use of AI, provide an excellent data structure for reliable genetic evaluation. The performance of a bull's daughters can be compared to that of other bulls' daughters across many environments.

Most dairy cows calve for the first time when they are two years old, and remain in the herd for an average of 4.5 lactations (DairyNZ, 2018a). The national herd contains approximately five million recorded milking cows, distributed over about 11,500 herds. Some 48% of the cow population is comprised of admixed cross-breeds among Holstein-Friesian and Jersey breeds. The predominantly straight-bred animals include 33.5% Holstein-Friesian, 9% Jersey, and 0.5% Ayrshire. The remaining 9% of the national dairy herd are other breeds and their crosses.

Given the large proportion of admixed cross-breeds, it is essential that genetic evaluations for NZ dairy cattle are produced using an across-breed evaluation. In addition to producing genetic evaluations (estimated breeding values [EBVs]) for cross breed cows and bulls, an across-breed genetic evaluation system also enables direct comparison of predominantly straight-bred Jerseys and Holstein-Friesians. The purpose of the national genetic evaluation system is to rank animals by their ability to produce profitable progeny, under pasture-based

management conditions. Farmers depend on the accuracy of across breed comparisons to generate and select the most profitable replacements for their farm system, irrespective of breed.
Animal rankings consider a number of a number of profit drivers, including milk production, beef production, feed intake, health, longevity and reproduction (Holmes et al., 2003). Holstein-Friesians and Jerseys are divergent for several of these traits, and it is critical that these differences are well characterised by the genetic evaluation system. Perhaps the most notable divergent traits are milk production and live weight. In the 2017/18 season the phenotypic difference between six-year-old Holstein-Friesians and six-year-old Jerseys was 110kg for live weight and 65kg for milk solids (DairyNZ, 2018a).

All other attributes held constant, increased milk production has a positive effect on farm profit, while increased live weight has a negative effect. Live weight is associated with beef revenue (income from culled cows and surplus calves) and feed costs. However, beef revenue from a heavier animal is small relative to the associated increase in feed costs. Accordingly, live weight has a negative economic value under the management conditions applicable to NZ dairy farmers (DairyNZ, 2013). Trade-offs between these and other traits are quantified using a selection index (Hazel, 1943). A lack of accuracy in the EBVs for divergent traits compromises the utility of this index for across breed comparison.

3.2. Selection Index

An animals influence on multiple profit drivers can be quantified using a selection index (Hazel, 1943). A selection index applies specific weighting to predictions of genetic merit for each of a number of traits, defining an objective system for ranking animals.

The selection index for the NZ dairy industry is called ‘Breeding Worth’ (BW). BW incorporates EBVs for milk production (milk fat, milk protein, milk volume), live weight, and five other economically important traits, namely: milk somatic cell score, live weight, body condition score, cow fertility, and cow survival

(DairyNZ, 2019a). These eight traits are key profit drivers of NZ dairy farm businesses.

3.2.1. Trait Weightings in Breeding Worth (BW)

The weighting factor on each of these eight traits is quantified in dollar units. The dollar weightings are determined based on the influence that each of these traits has on key profit drivers. These weightings, current for September 2019, are shown in Table 1 (DairyNZ, 2019c).

Table 1 Weighting factor applied to each trait in Breeding Worth.

Trait	***September 2019 economic weight***
Milk Fat	$3.49/kg
Milk Protein	$4.38/kg
Milk Volume	-$0.092/L
Mature Live weight	-$1.3kg
Residual Survival	$0.112/day
Somatic Cell Score	-$37.3/SCS*
Fertility	$5.88/CR42**
Body Condition Score	$96.3/Score***

Note. * = SCS: Herd testing measures Somatic Cell Count (SCC) which is log-transformed to produce the SCS phenotype. ** = CR42: Percent of progeny calving within the first 42 days of the calving period. *** = Score: Body condition score is subjectively assessed by trained inspectors on a scale of 1 to 10.

3.3. Genetic Improvement

Genetic improvement within any given population is collectively determined by the accuracy of selection, intensity of selection and generation interval, as in Equation 1, where ΔG is the rate of genetic improvement (Rendel & Robertson, 1950).

$$\Delta G = \frac{accurary\ of\ selection * intensity\ of\ selection}{generation\ interval} \qquad \text{Equation 1}$$

3.3.1. Selection Intensity

The intensity of selection is dictated by the proportion of available animals that are selected for breeding. Selection intensity is highest where the number of

animals selected is small relative to the total number of candidates. Selection intensity is typically much higher for bulls compared to cows. Therefore, bulls are the major avenue for genetic improvement despite the fact that both sexes contribute equally to the next generation of replacements.

Selection intensity for the dams of replacement cows (e.g. young cows whose role is to maintain herd size by replacing culled animals) is limited. Only healthy females born early in the calving season are reared as replacements, often irrespective of the merit of their dam. In addition, there is a high incidence of involuntary culling (i.e. culls that could not be avoided) on most NZ dairy farms. Involuntary culling leaves little room for 'voluntary' culling of inferior animals, as farmers look to minimise the proportion of the herd that is culled each year. Selection intensity is much higher for the dams of replacement bulls, as only around 400 bull calves are purchased by breeding companies each year (DairyNZ, 2019b).

In contrast, selection intensity for bulls is very high. Widespread use of Artificial Insemination (AI) technology can allow 100,000 or more inseminations from one bull in one year, such that relatively few sires are required to produce each new generation of dairy cattle. Breeding companies have the opportunity to select a proportionately small number of top-ranking candidate bulls.

3.4. Accuracy of Selection

Accuracy of selection describes the strength of the relationship between the EBVs the true breeding values (TBVs). The TBV of an animal can be viewed as the sum of three components. First, half the genetic merit of the animal's sire. Second, half the genetic merit of the animal's dam. Third, the effect of Mendelian sampling on the individual animal.

Mendelian sampling describes the random aspects of inheritance, whereby an animal can inherit more or less than half of the superior genome fragments from either parent. The effect of Mendelian sampling is to produce offspring that exhibit a deviation from their parent average. In a pedigree-based genetic evaluation system, information on the effect of Mendelian sampling on an

individual can be obtained via phenotype measurements on the animal itself, or the animal's progeny.

It is important to note that the apparent average genetic merit of an animal's progeny will be influenced by Mendelian sampling, especially if only few progeny contribute to that average. Sufficient progeny must be considered to ensure that the observed average effect of Mendelian sampling represents the expected value of zero. Otherwise the progeny mean will be biased relative to the true parent average.

The formula for computing the accuracy of EBVs for progeny tested bulls is shown in Equation 2 (Robertson, 1957), where n is the count of daughters and h^2 is the trait heritability.

$$\text{Accuracy of selection (progeny test)} = \sqrt{\frac{\frac{1}{2}nh^2}{1+\frac{1}{4}(n-1)h^2}} \qquad \text{Equation 2}$$

Delaying selection of animals in order to base the selection on progeny information will increase the interval between generations. The extent of this time delay will depend on the age of the animal when it reaches sexual maturity, and the age the progeny must be to express the phenotype. For example, where phenotypes are collected over the course of a daughter's first lactation, bulls will be four years old when their progeny tested EBVs based on those data are available.

3.5. Generation Interval

In well managed selection programs, each new generation should be superior to the previous one. An optimal rate of genetic improvement will occur where the interval between generations is minimised, whilst accuracy of selection is maintained.

Phenotypes measured earlier in an animal's life, and/or technologies, such as genomic selection, facilitate a shorter generation interval for bulls. Shortening the generation interval will have a significant effect on the rate of genetic

improvement. Adolescent live weight is available earlier in an animal's life (relative to the current predictor phenotype, live weight during lactation). If adolescent live weight is an accurate predictor of live weight during lactation, including this phenotype as a predictor for the live weight EBV could increase the accuracy of BW. This increase in BW accuracy will translate into an increased rate of genetic progress.

3.6. Data to Predict Estimated Breeding Values

Farmers are responsible for generating the majority of phenotype data used for genetic evaluation. Herd test records, and all other phenotypes required for genetic evaluation are stored in the Dairy Industry Good Animal Database (DIGAD). The data repository (and genetic evaluation system) are the responsibility of New Zealand Animal Evaluation Limited (NZAEL) a wholly owned subsidiary of the farmer funded, industry-good body known as DairyNZ. In addition to phenotype data recorded in NZ, international collaboration for some selection traits allows the EBVs produced overseas to inform NZ EBVs. This international collaboration is facilitated by an organisation called 'Interbull' (See section 3.6.2).

Phenotypes can be characterised as 'routine' or 'non-routine' (Table 2). 'Routine' describes information that farmers collect as part of normal farm practice, for example herd test data. These data usually have application outside of genetic evaluation. 'Non-routine' describes information that is generated specifically for the purpose of genetic evaluation. Farmers do not have an immediate need for non-routine data for day-to-day farm management. Table 2 shows the information currently used to predict each of the EBVs that contribute to the national selection index, Breeding Worth.

3.6.1. Phenotype Data Coordination

It is important that each bull in a breeding programme has sufficient phenotyped daughters to enable robust evaluation of his genetic merit. Consistent volumes of phenotype data for young bulls are achieved though coordinated progeny testing schemes. These schemes involve a network of farmers who are incentivised to use young bulls with predicted EBVs (and thus BWs) of low

reliability. Farmers are incentivised to record key phenotype data, and these data are used to improve the reliability of the EBVs for the sires of their cattle. Well-designed progeny testing schemes strengthen the accuracy of prediction in a coherent manner, taking due account of the cost-effectiveness of measuring phenotypes to increase the accuracy of all EBVs that comprise the selection index.

Table 2 Type of phenotypes to predict Breeding Worth (BW) estimated breeding values (EBVs).

EBV	**Phenotype**	**Phenotype type**	**Age of cow (years)**	**International collaboration***
Milk production - Fat - Protein - Volume	Milk testing	Routine	2-3	yes
Somatic cell score	Milk testing	Routine	2-3	yes
Fertility	- Calving dates - Mating dates	Routine	2-3	yes
Survival	Herd exit dates	Routine	2-3	yes
Mature Live weight	- Scale weight - Inspector*** weight scores	Non-routine	2-3	no
Body condition score	Inspector*** condition scores	Non-routine	2-3	no

Note. * = Where international collaboration is in place, estimated breeding values (EBVs) produced overseas can be used to inform NZ EBVs. *** = Inspectors are trained to assign visual scores as a measure of weight and body condition.

Although highly effective, progeny testing schemes are expensive and logistically challenging to coordinate. Larger AI companies can justify operating progeny testing schemes more frequently than their smaller competitors, as the cost of generating daughters and phenotypes can be recuperated through vast

semen sales for successful bulls. In a progeny-based genetic evaluation system, higher accuracy, ‘daughter proven’ EBVs provide farmers with confidence to invest in the generation of offspring from individual bulls. Bulls that rank highly based on these initial progeny test EBVs are generally used extensively, and it is not uncommon for an individual bull to have over 100,000 inseminations. This widespread use based on progeny test EBVs occurs when a bull is five years old, and leads to an influx of routine phenotype data three years later, when he is eight. The accumulation of these routine data are accompanied by an increase in EBV accuracy for the corresponding BW traits.

Smaller AI companies that do not coordinate progeny testing schemes tend to rely on routinely collected data to strengthen the accuracy of the EBVs for their bulls. For EBVs with routinely collected predictor phenotypes, this ad-hoc approach can achieve a similar outcome to coordinated progeny testing, but the number of daughter phenotypes recorded may be delayed and/or inconsistent. Non-routine phenotypes present a bigger problem, however, as there is no mechanism for generating daughter phenotype data. Therefore, EBVs predicted by non-routine phenotypes, such as mature live weight and body condition score (BCS), often have low accuracy for the entire life of the bull when formal progeny testing is not in place.

International bulls that are used locally present a good example of this problem, as breeding companies responsible for importing sperm do not tend to coordinate progeny testing schemes in New Zealand. This lack of data is illustrated by Figure 1, which shows the distribution of live weight daughter numbers, by the sire’s country of origin.

3.6.2. International Collaborations: Accuracy of Selection for Imported Bulls

International collaboration can improve the accuracy of EBV for bulls with daughters overseas. The NZ dairy industry is a member of an international genetic evaluation organisation called Interbull. The purpose of Interbull is to facilitate the exchange of genetic predictions across counties. Foreign bulls often have daughter phenotypes measured overseas prior to their semen being

imported to NZ. This collaboration allows imported bulls to be ranked more accurately in NZ based on their relative rankings from daughters off-shore. In practice, the value of international EBV data can be limited in NZ, as the seasonal and pastoral characteristics of the NZ dairy industry generally lead to poor correlations in EBV rankings between NZ and most other countries. In addition to these poor correlations with other countries, Interbull does not process all of the EBVs that are included in BW. The BW traits processed by Interbull are indicated in Table 2. The most notable omitted trait is mature live weight, which is an important component of selection decisions in NZ.

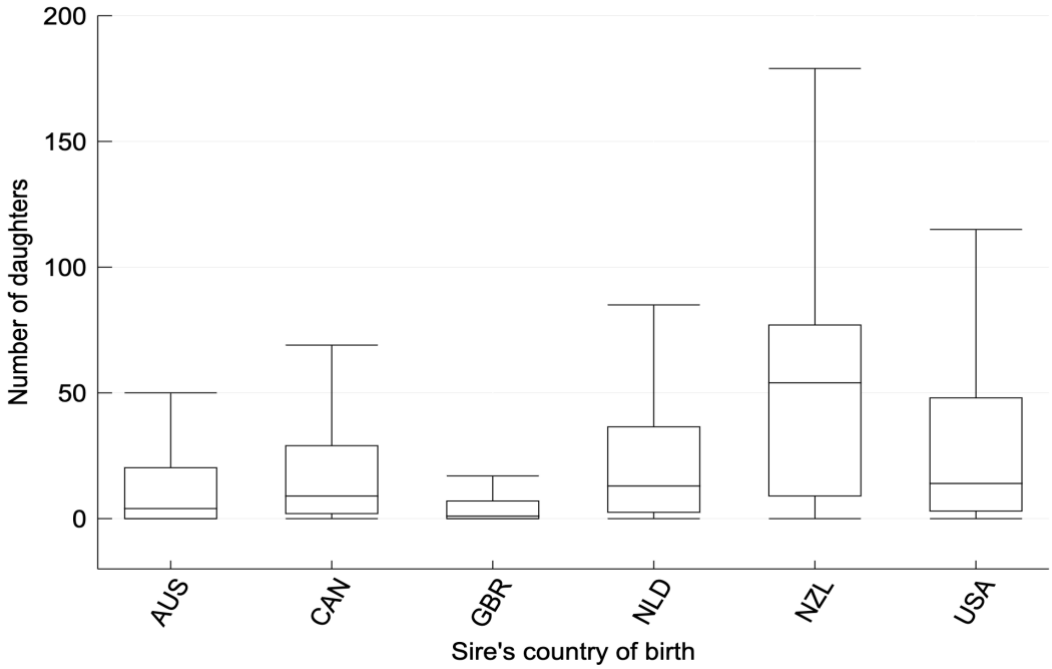

Figure 1 Number of NZ born daughters per sire with lactation live weight phenotypes.
Sires are grouped by their country of birth (DairyNZ, 2019b). Note. Includes sires with at least one herd tested daughter, from countries with at least 100 bulls enrolled with NZAEL. AUS: Australia (409 bulls), CAN: Canada (658 bulls), GBR: Great Britain (242 bulls), NLD: The Netherlands (363 bulls), NZL: New Zealand (15,577 bulls), USA: United States of America (1,448 bulls).

3.6.3. Mature Live Weight – Predictor Phenotype Opportunity

Mature live weight is one of the two BW EBVs to have a non-routine predictor phenotype (i.e. live weight during lactation). In addition to having a predictor phenotype that is difficult to obtain, this trait is not included in international data

sharing collaborations. These two factors lead to inaccurate mature live weight EBVs for many international sires.

In recent years, farmers have been encouraged to more carefully manage the rearing of young stock. It is now common for farmers to pay close attention to the live weight of their young animals, as a means of monitoring growth. This behaviour change may have been encouraged by NZ-based research that demonstrated the improved lifetime productivity of young stock that consistently meet growth targets in early life (Van Der Waaij, Galesloot, & Garrick, 1997). This increased vigilance in achieving growth targets may present an opportunity for improving the genetic evaluation of mature live weight, as a data set including hundreds of thousands of adolescent live weight phenotypes is accumulating. Figure 2 shows the trend of increased availability of live weight phenotype measures from adolescent animals. Around 30% of replacement heifers are now weighed at least once during their adolescence. We hypothesise that these adolescent live weight phenotypes could provide an accurate predictor phenotype for the mature live weight EBV.

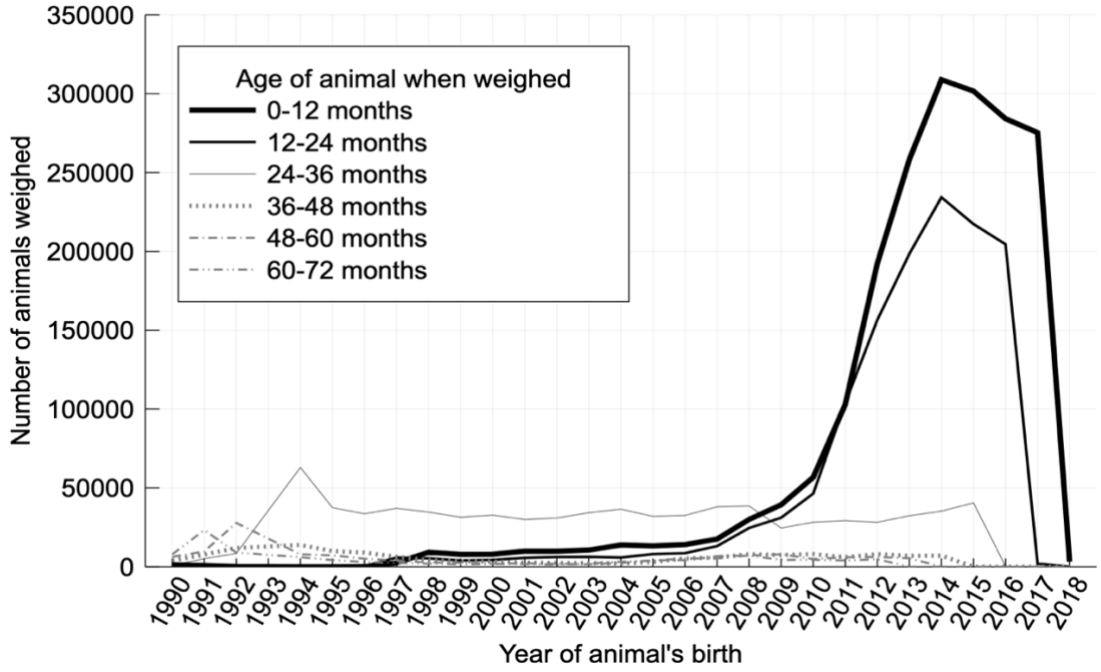

Figure 2 Number of animals weighed by birth year, and age when weighed. Data source: DairyNZ, June 2018. Note: animals weighed in multiple age categories were included in the count for each relevant age category.

3.6.3.1. Multi-use Phenotype

Farmers are able to gain value from the adolescent live weight phenotype in multiple ways, which improves the likelihood that they will invest in measuring it. An improved business case for measuring live weight data could significantly increase the number of animal's contributing live weight phenotypes for genetic evaluation. Appropriate phenotype measures on individual cows provide an indication of the effect of Mendelian sampling for that animal. If a greater proportion of the national herd were contributing phenotypes, the accuracy of forward predicted (parent average) EBVs would increase, because dam EBVs would be more accurate. In addition to this benefit, the investment from breeding companies for targeted phenotype generation may no longer be required. Similarly, small breeding companies would gain more accurate EBVs for their bulls, despite not actively collecting live weight data.

3.6.3.2. Earlier Phenotype

The improved timing of adolescent live weights can be seen in Figure 2. On the data of this data extract (June 2018), 2016 and 2017 born animals were too young to have first lactation live weights, but over 200,000 animals in each of these birth years had adolescent live weights measured. Live weight phenotypes that can be obtained before first lactation can provide an earlier indication of the Mendelian sampling effect for that animal. Farmers may choose to use this information when selecting herd replacements. In addition, earlier daughter phenotypes will strengthen the accuracy of EBVs for bulls at a younger age. Improved EBV accuracy for younger bulls will shorten the interval between generations, as breeding companies can eliminate candidate bulls from their breeding programmes earlier. Where the generation interval can be shortened without compromising selection accuracy, the rate of genetic gain for a trait—in this case, mature live weight—will increase (Rendel & Robertson, 1950).

3.7. Present Research

The aim of our research was to determine the utility of adolescent live weight for predicting live weight during first lactation. We addressed this research aim using two approaches. The first study characterised the (co)variation of live

weight in NZ Holstein-Friesians classified into four age categories (181 to 940 days of age). We predicted that the genetic correlations between live weight at these four ages would be strong and positive. The second study aimed to demonstrate the value of a prototype live weight EBV, where adolescent live weights are included. We compared the accuracy of first lactation EBVs produced with versus without adolescent live weight phenotypes. We predicted that the use of adolescent live weights would improve the accuracy of the live weight EBV.

The current national mature live weight EBV is obtained from a repeated measures analysis. Live weights from first lactation and beyond are treated as repetitions of the same trait (Holmes et al., 2003). Live weight phenotypes obtained during first lactation are the most prominent, because coordinated progeny testing schemes prioritise collecting phenotypes during this lactation. In this thesis, we focus on associations between adolescent weights and weights during first lactation for which large datasets are available. We assume that a strong relationship with live weight in first lactation is indicative of a strong relationship with live weight in subsequent lactations.

4. Study One: (Co)Variance Parameters for Live Weight at Different Ages in New Zealand Holstein-Friesian Cattle.

4.1. Abstract

The purpose of this study was to determine the extent to which cattle live weights across ages (co)vary. We classified live weight phenotypes into four categories based on the age of the animal when it was weighed. The age categories were as follows: 181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW). We completed a series of pair-wise bivariate analyses to estimate the residual and genetic covariances between each age category. Our analyses considered only Holstein-Friesian animals. We hypothesised that genetic (co)variances between live weight at different ages in the NZ Holstein-Friesian population would be strong and positive. We observed large genetic correlations ranging from 0.79 to 0.97 between each age category. These genetic correlations support the inclusion of adolescent live weight as a predictor of live weight in first lactation.

4.2. Introduction

New Zealand Animal Evaluation Limited (NZAEL) is responsible for producing a selection index for recorded cows and bulls in New Zealand (NZ). Producing this selection index involves estimating breeding values (EBVs) for all of the eight selection index traits, one of which is mature live weight. The mature live weight EBV is currently predicted using live weights collected during lactation (Holmes et al., 2003). Adolescent live weights could provide an earlier and more frequently measured predictor phenotype for the live weight EBV.

Previous research in NZ dairy cattle has found that live weights measured at different ages through adolescence are moderately heritable, and exhibit genetic correlations close to 1. Pryce, et. al. (2011) obtained heritabilities of 0.44 (+/-0.10) for live weight at 250 days (8.2 months) of age in a population of 1000 well recorded Holstein-Friesian heifers in New Zealand. Weights at other ages were not investigated, and so the study did not report covariances. A more comprehensive study completed by Van der Waaij et. al. (1997)

estimated heritabilities, phenotypic correlations and genetic correlations for live weight at three pre-lactation ages (shown in Table 3). Live weight during first lactation was not investigated.

Table 3 Heritabilities (diagonal), phenotypic (above the diagonal) and genetic (below the diagonal) correlations with accompanying standard errors (presented in brackets) observed in 2365 NZ born animals.

Age (Months)	**9**	**15**	**21**
9	0.39 (0.12)	0.83 (0.01)	0.72 (0.02)
15	0.98 (0.03)	0.52 (0.14)	0.81 (0.01)
21	0.93 (0.05)	0.93 (0.04)	0.62 (0.15)

Note. Analysis included multiple breeds (36% Holstein-Friesian, 34% Jersey, 15% Reds, and 15% Cross-breeds; table adapted from Van Der Waaij et al., 1997).

International research has shown similar results, although reported correlations between live weights at different ages tend to be lower (Table 4). The majority of this international research has been completed in beef cattle.

(Co)Variance parameters can vary between populations. International research provides an indication of what we would expect to see in NZ dairy animals, but it is important that these values are obtained specifically in the NZ dairy context. Thus, we used live weight data from NZ Holstein-Friesians to quantify the (co)variance parameters of live weight at four age classifications. We hypothesised that the relationship between live weight across ages in NZ dairy cattle would be strong and positive.

Table 4 Heritabilities, phenotypic (above the diagonal) and genetic (below the diagonal) correlations between live weight at various ages, as reported in international research.

	Age Category (Months)						
Age Category		**0 (Birth)**	**1 to 5**	**6 to 10**	**10 to 17**	**18 to 22**	**23 +**
	0 (Birth)	0.49(3) 0.53(4) 0.25(5) 0.46(6) 0.41(7) 0.48(8)	0.79(6)	0.41(2) 0.73(4) 0.29(5) 0.30(7)	0.40(2) 0.27(5) 0.33(6) 0.29(7)	0.31(7)	0.33(3) 0.30(7) 0.30(4)
	1-5	0.79(6) 0.63(8)	0.49(6) 0.30(8)		0.62(6)	0.62(6)	
	6-10	0.60(2) 0.79(4) 0.36(5) 0.66(7) 0.52(8)	0.69(8)	0.33(1) 0.24(3) 0.45(4) 0.34(5) 0.51(6) 0.12(7) 0.36(8)	0.40(5) 0.73(7) 0.76(2)	0.63(7) 0.81(1)	0.32(3) 0.29(7) 0.43(4)
	10-17	0.55(2) 0.44(5) 0.53(6) 0.54(7) 0.39(8)	0.84(6) 0.59(8)	0.90(2) 0.59(5) 0.92(7) 0.66(8)	0.37(1) 0.30(3) 0.28(5) 0.51(6) 0.23(7) 0.49(8)	0.79(7)	0.46(3) 0.45(7)
	18-22	0.61(7) 0.32(8)	0.45(8)	0.9(7) 0.80(1) 0.56(8)	0.97(7) 0.70(8)	0.28(7) 0.36(8)	0.54(7)
	23+	0.64(3) 0.62(7) 0.50(4) 0.11(8)	0.12(8)	0.8(3) 0.49(7) 0.59(4) 0.18(8)	0.76(3) 0.68(7) 0.30(8)	0.77(7) 0.40(8)	0.39(7) 0.75(4) 0.32(8)

Note. 1 (Boligon et al., 2010), 2 (Bourdon & Brinks, 1982), 3 (Bullock, Bertrand, & Benyshek, 1993), 4 (Coffey, Hickey, & Brotherstone, 2006), 5 (Gregory, Cundiff, & Koch, 1995), 6 (Groen & Vos, 1995), 7 (Meyer, Johnston, & Graser, 2004), 8 (Evans, Kearney, McCarthy, Cromie, & Pabiou, 2014).

4.3. Materials and Methods

4.3.1. Overview

We classified the live weight data into four categories based on the age of the animal when it was weighed. The categories were as follows: 181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW). We produced the covariance parameters between each of these age categories using bi-variate linear mixed models. Six bivariate analyses were completed, with each age category included in three analyses.

4.3.2. Data

Pedigree and phenotype data were provided by DairyNZ in June 2018. Access to these data was approved by the New Zealand Dairy Industry Data Access Panel, an independent panel that presides over access to core fields stored in the Dairy Industry Good Animal Database (DIGAD). Animal ethics approval was not required as these analyses made use of existing data.

We applied a number of data filters to confine the scope of the study, and improve data quality. A summary of the inclusion criteria is as follows.

- Animal was predominantly Friesian or Holstein.
- Animal was Female.
- Animal was born after 1995.
- Animals age in days at the time the weight was measured was within one of the defined age categories (181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW).
- One live weight record per animal per age category.
- Live weight observations were within three standard deviations of the contemporary group mean.

For full details on data filtering, see Section 9.1.1.

4.3.3. Age Categories

We created four age categories according to the age of the animal when it was weighed. We defined these age categories based on the growth curve we observed in the data. The objective was to categorise the traits in such a way that weight change was approximately linear across ages within each category (Figure 3).

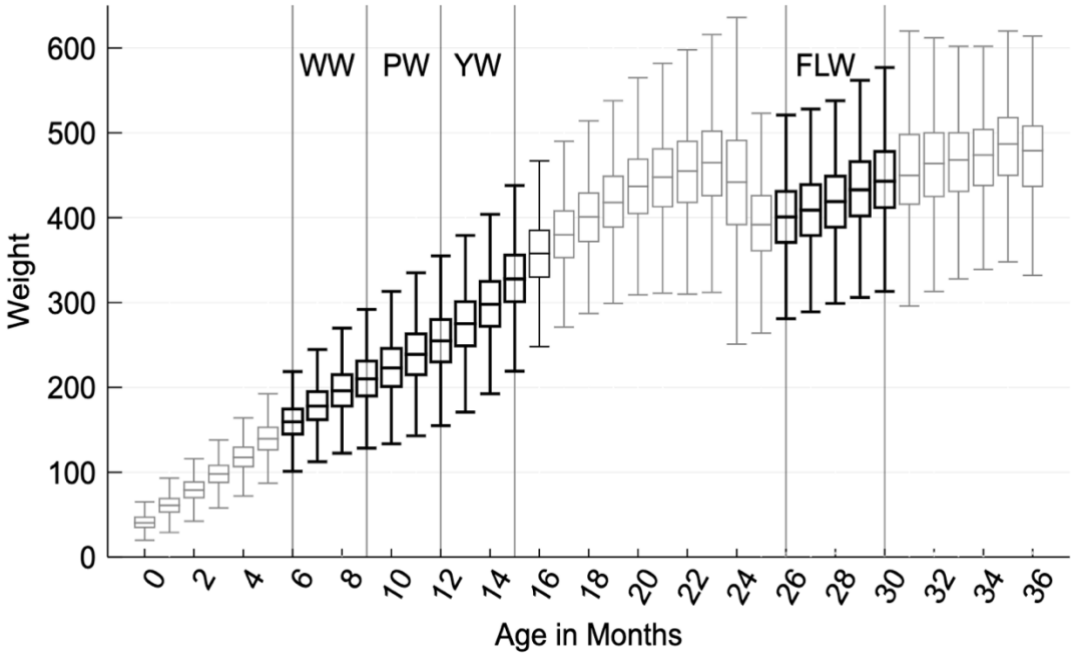

Figure 3 Mean weights for Holstein-Friesian females born after 1995. Boxplot outlines show whether data were included (black) or excluded (grey) in subsequent analysis. The vertical gridlines and annotations show approximately how these data were categorised into traits. 181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW).

4.3.4. Model Equation

We fitted a linear mixed model to complete each of the six bivariate analyses. The matrix representation of the linear mixed model equation is:

$$\mathbf{y_i} = \mathbf{X_i b_i} + \mathbf{Z_i u_i} + \mathbf{e_i} \qquad \text{Equation 3}$$

where $\mathbf{y_i}$ is a vector of phenotypes for the i_{th} age category (WW, PW, YW, FLW), $\mathbf{b_i}$ is a vector of fixed effects for the i_{th} age category, $\mathbf{u_i}$ is a vector of breeding values (random effects) for the i_{th} age category. The vector $\mathbf{e_i}$ is a

vector of residuals corresponding to each of the observations in the i_{th} age category. $\mathbf{X}_i$ is an incidence matrix relating each phenotype record in the i_{th} age category to the relevant fixed effects. $\mathbf{Z}_i$ is an incidence matrix relating phenotypes to their corresponding breeding value, with a row for each phenotype in the i_{th} age category and a column for each animal represented in $\mathbf{u}_i$. For a full description of this model, including location and dispersion parameters, see Section 9.2.

4.3.5. Missing Values

Animals were included in the analysis if they, or a member of their contemporary group had a live weight phenotype in both age categories. Including these animals with missing data allowed the analysis to account for non-random missing data (Apiolaza, Gilmour, & Garrick, 2000).

4.3.6. Fixed Effects/Covariates

All analyses included contemporary group as a fixed effect and age in days as a fixed covariate. Lactation day was included as an additional fixed covariate where the phenotype belongs to the first lactation weight (FLW) category. This age category includes weights obtained following an animal's first calving.

4.3.6.1. Contemporary Groups

A contemporary group was defined as a group of animals weighed on the same day, at the same location, from the same herd. Data used were herd number (a sequential number assigned to each distinct herd that is present at a location), latitude and longitude coordinates of farm location, and weigh date. The contemporary group identifier was included in all model equations as a fixed class effect. See appendix 9.1.2 for the count of contemporary groups in each univariate analysis.

4.3.6.2. Age in Days as a Fixed Covariate

The age of an animal was expressed as the deviation from the mid-point age of the relevant category (the age in days halfway between the lower and upper age cut off). Following this pre-processing step, estimates of the contemporary group effects represent the least squares means. In addition, expressing the

age of an animal as a deviation from the mid-point reduces the covariance between estimates of the contemporary group effects and the effect of age in days, thus improving the numerical conditioning of the model equations.

4.3.6.3. Lactation Day as a Fixed Covariate

Lactation day is defined as the days between an animal's calving date and the date the weight record was obtained. The lactation day fixed effect was only applied to the FLW category.

4.3.7. Software

Command line bash scripts were generated to pre-process phenotypic and pedigree data. Genetic analysis and post-processing were performed using the statistical software Julia (*The Julia Language*, 2019) The package add-on JWAS (Cheng, 2019) was used for genetic analysis. The post-processing of results was carried out using the packages CSV, Statistics, LinearAlgebra, StatsPlots, DataFrames, DelimitedFiles, Distributions, Measures. See Section 11 for scripts.

4.3.8. Solver

A single site Gibbs sampler, using a Markov-chain Monte Carlo (MCMC) technique was used to obtain samples of the posterior distributions for effects in the mixed model equations, and the variance components used to build the mixed model equations. Each MCMC iteration directly sampled plausible values for the fixed effects, then random effects other than the residuals, then the polygenic variance and residual variance, and in the case of the bivariate models, polygenic co-variance and residual co-variance. That sampling was then continued for up to 90,000 iterations to make inference using the posterior means and posterior variances of these samples.

4.3.9. Prior and Starting Values

Prior values for variance parameters were estimated based on previous literature, phenotypic variances observed in the current dataset and preliminary analysis completed as part of this study (Figure 4).

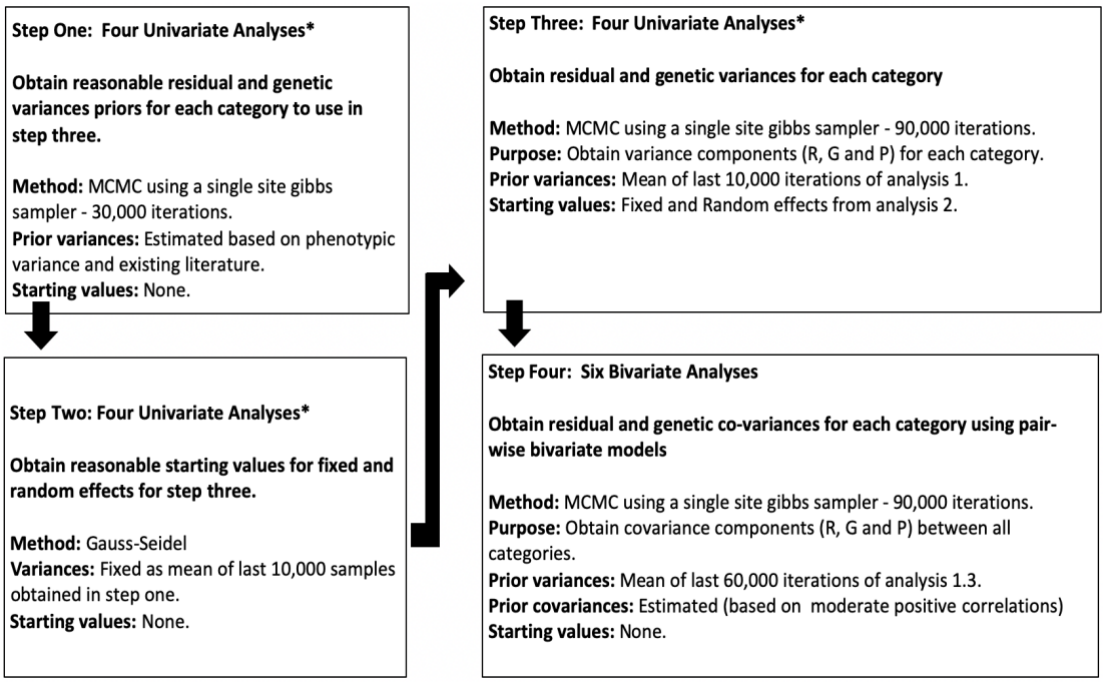

Figure 4 Work flow of analyses to obtain suitable prior and starting values, and complete six bivariate analyses.
*The model used to complete these univariate analyses is described in Section 9.2.

4.3.10. Burn-in Period

A fixed number of iterations per analysis were disregarded from the results as a burn-in period. The purpose of a burn-in period is to ensure that the MCMC inferences included in the results of the analysis come from a stable distribution. The length of the burn-in periods for the bivariate analyses was 30,000 iterations. Each burn-in period was established by grouping the MCMC inferences consecutively, and then observing the change in distribution over time. For example, the first grouping was iteration 1 to iteration 10,000, the second grouping was iteration 10,001 to iteration 20,000, and so on. The distribution of MCMC inferences from one age category to the next consistently overlapped once the models were stable. This method is based on the convergence criteria described by Geweke (1992), which suggest that a model is stable if the posterior mean of early results is not different to the posterior mean of later results.

4.3.11. Credibility Intervals

We calculated credibility intervals for the posterior means of MCMC samples that were symmetric around the mean. The upper bound was the 97.5th percentile of the MCMC sample solutions and the lower bound was the 2.5nd percentile of MCMC sample solutions. These intervals contain 95% of the probability for the inference presented (Blasco, 2017). The credibility intervals excluded MCMC sample solutions produced during the burn-in period for each model.

4.4. Results

4.4.1. Covariances Between Live Weight at Different Ages

Covariances were estimated using a series of six bivariate analyses (Table 5). Where both age categories were adolescent weights (WW with PW, WW with YW, PW with YW), approximately 100,000 animals were contributing phenotypes to both age categories. These 100,000 animals represented around 600 sires. For each of the bivariate analyses including the FLW category (WW with FLW, PW with FLW, YW with FLW), approximately 4,000 animals were contributing phenotypes to both age categories. These 4,000 animals represented between 50 and 90 sires. See Section 9.1.3 for more detail.

The estimated genetic correlations between live weight at different ages ranged from 0.79 to 0.97 (Table 5).

Table 5 Phenotypic (above the diagonal) and genetic (below the diagonal) correlations with accompanying upper and lower credibility intervals (presented in brackets).

Category	WW	PW	YW	FLW
WW		0.80 (0.79, 0.80)	0.72 (0.72,0.73)	0.58 (0.56,0.60)
PW	0.96 (0.96, 0.97)		0.83 (0.82,0.83)	0.56 (0.54,0.58)
YW	0.93 (0.91,0.94)	0.97 (0.97,0.98)		0.67 (0.65,0.69)
FLW	0.80 (0.70,0.86)	0.79 (0.67,0.90)	0.85 (0.79,0.91)	

Note. WW = 181 days to 280 days, PW = 281 days to 380 days, YW = 381 days to 480 days, FLW = 791 days to 940 days.

4.4.2. Heritabilities

Each trait was involved in three bivariate analyses, and so heritabilities were produced three times for every trait (Table 6). Animals were included in each bivariate analysis if they, or a member of their contemporary group, had phenotypes in both categories. Not all contemporary groups were weighed in all categories. Therefore, the population of animals included in each bivariate analysis was slightly different and there was variation in the heritabilities observed. The bivariate models involving FLW had substantially fewer animals included than those involving two adolescent live weights, which resulted in much wider creditability intervals for these heritability estimates. The credibility intervals of all heritability estimates overlapped.

Table 6 Heritability estimates with accompanying upper and lower credibility intervals (presented in brackets) of live weight for four age categories.

Category	**WW**	**PW**	**YW**	**FLW**
WW		0.33 (0.29, 0.34)	0.37 (0.35,0.40)	0.48 (0.39,0.59)
PW	0.32 (0.3,0.34)		0.35 (0.31,0.39)	0.45 (0.36,0.54)
YW	0.32 (0.30, 0.34)	0.30 (0.27,0.33)		0.46 (0.36,0.55)
FLW	0.33 (0.26,0.40)	0.31 (0.22,0.38)	0.37 (0.30,0.45)	

Note. WW = 181 days to 280 days, PW = 281 days to 380 days, YW = 381 days to 480 days, FLW = 791 days to 940 days. The heritability presented corresponds to the column header. The row header shows the second trait in the bivariate analysis that estimated the presented heritability.

4.5. Discussion

4.5.1. Research Summary

The purpose of this study was to quantify the genetic (co)variances of live weight in different age classes of NZ Holstein-Friesian cattle. We hypothesised that genetic covariances would be strong and positive. The results of our analysis indicate that genetic correlations between live weight at different ages range from 0.79 to 0.97. The heritability of live weight across the four age categories ranged from 0.30 to 0.48. The trend was for the heritability of live weight to increase with age.

The results presented in this study align with previous literature, which indicated that genetic correlations between adolescent live weights in NZ cattle range from 0.93 to 0.98 (Van Der Waaij et al., 1997) and heritabilities range from 0.39 to 0.62 (Pryce et al., 2012; Van Der Waaij et al., 1997). Van der Waaij et al. (1997) observed that heritabilities increase with age, which is consistent with our findings. Our research reports the first covariances between adolescent live weights and live weight during first lactation for NZ dairy cattle.

Internationally, live weight variance parameters are more readily available, especially in beef cattle. Various studies report heritability estimates ranging from 0.10 to 0.75 (Boligon et al., 2010; Bourdon & Brinks, 1982; Bullock et al., 1993; Coffey et al., 2006; Evans et al., 2014; Gregory et al., 1995; Groen & Vos, 1995; Meyer et al., 2004). Overall, covariances between live weights at different ages were weaker in international populations, relative to covariances we observed in our data. The reasons for this difference between NZ and international populations are not clear. One explanation is that the farming structure in NZ is more ideal for measuring genetic variance. The majority of animals are born within a short time frame (approximately three months), and reared in large, stable contemporary groups (Section 3.1). Therefore, the environmental variance is both decreased, and more easily recognised. This data structure may not be as prevalent in international data-sets.

4.5.2. Limitations

This study was limited to Holstein-Friesian animals. The majority of pure-bred dairy cattle in NZ are Holstein-Friesian. However, a greater proportion of animals are admixed Holstein-Friesian and Jersey (Section 3.1). The (co)variances of live weight across ages within the Jersey breed were not examined in the current research. Previous research has shown strong positive genetic covariances between live weight across age classes, in a multi-breed context (Van Der Waaij et al., 1997). It is likely that the findings of the current research will extend to other breeds in NZ. This could be confirmed by repeating this study with Jersey and Cross-breed animals.

The covariances produced in this study quantify the accuracy of adolescent live weight phenotypes as a useful predictor trait for a ‘first lactation live weight’ EBV. In practice, the covariances between adolescent live weight and mature live weight are of more relevance, as the current live weight EBV in NZ is designed to represent mature live weight. Unfortunately, very few animals have both mature and adolescent weights and so a robust analysis of these genetic (co)variances was not possible. Our assumption is that given FLW data is adding value to the current mature live weight EBV, a trait with a strong genetic association with FLW can also add value. If obtaining the variance parameters between adolescent and mature live weights is a priority, a data collection initiative will be required. Animals that were weighed during adolescence would need to be weighed again as mature cows.

The numeric condition of the mixed model equation could be improved by converting the lactation day (Section 4.3.6.3) fixed covariate to a deviation from a mid-point day of lactation. This has not been done in the current analysis.

4.5.3. Practical Implications and Future Directions

Adolescent live weight is a likely predictor of live weight in first lactation. These phenotypes are available earlier in an animal’s life, and so including them as a predictor trait may result in accurate earlier genetic selection for the live weight trait. Selection earlier in life will shorten the generation interval. The rate of genetic gain will increase where the generation interval can be shortened without compromising accuracy of selection.

In addition to providing a useful predictor trait for pedigree based EBVs, adolescent live weights may also improve the accuracy of genomic EBVs. The high genetic correlations between adolescent live weights and first lactation live weight indicate that animals with adolescent live weight phenotypes could contribute meaningful information to a genomic reference population. Including these adolescent live weights in a genomic reference population would increase the statistical power of genomic predictions, and potentially allow less common genotypes (i.e. those of international sires) to become represented.

The next step for this research was to quantify the value of including adolescent live weight as a predictor phenotype for pedigree based live weight EBVs. This analysis is summarised in Section 5 of this thesis.

5. Study Two: Estimating Live Weight Breeding Values Using Adolescent Live Weight Phenotypes

5.1. Abstract

Adolescent live weight observations are not currently used to predict estimated breeding values (EBVs) for mature live weight in the New Zealand (NZ) dairy industry. The results of our earlier study (discussed in Section 4), indicated that genetic correlations between live weight across age classes are strong and positive. Therefore, adolescent live weight phenotypes are likely to add value as a predictor trait for a mature live weight EBV. The objective of this study was to demonstrate the utility of adolescent live weight in predicting first lactation live weight (FLW) EBVs. We hypothesised that the inclusion of adolescent live weight phenotypes as predictors of a FLW EBV would improve the accuracy of the EBV, compared to using FLW phenotypes alone. We tested this hypothesis by producing EBVs from two analyses. The first was a univariate analysis, including only FLW phenotypes as predictor traits. The second was a univariate repeated measures model, including both adolescent and FLW phenotypes. In each analysis, the FLW phenotypes were excluded for animals born in 2015. The correlations between EBVs and omitted FLW phenotypes were used to quantify the accuracy of EBVs produced by each analysis. The correlations between parent average EBVs and omitted FLW phenotypes were similar across both analyses (0.27 and 0.28). A subset of the 2015 born animals in the repeated measures analysis had a dam contributing an adolescent live weight. The correlation between parent average EBVs for this subset and omitted FLW phenotypes was 0.34. A further subset of 2015 born animals had an adolescent live weight phenotype that could contribute to their EBV. Where these adolescent live weights were included, the correlation between EBVs and FLW phenotypes lifted to 0.59. These results indicate that inclusion of adolescent live weight will improve the accuracy of the live weight EBV for Holstein-Friesian cattle in NZ.

5.2. Introduction

In New Zealand (NZ), breeding values for live weight are estimated using weight phenotypes collected during lactation. It is uncommon for farmers to

weigh cows during lactation and so relatively few cows have lactation live weight phenotypes recorded. Approximately one million replacement dairy heifers are recorded each year, and fewer than 40,000 of them go on to be weighed during lactation. Most of these lactation live weights result from data collection programs operated by the two major breeding companies in NZ (LIC and CRV). Live weight measured during lactation provides a predictor trait for the mature live weight EBV (Holmes et al., 2003) but these data have limited value outside of genetic evaluation and are expensive to obtain. In addition, any time delay in waiting for offspring to reach first lactation extends the generation interval for this trait.

A new opportunity for improving the prediction of mature live weight EBVs is emerging, as farmers are increasingly weighing adolescent animals (24 months old and younger). The growth rate of young cattle has been shown to have a lasting effect on cow productivity (Van Der Waaij et al., 1997). Therefore, farmers are motivated to measure adolescent live weight as a means of monitoring growth. Over the last ten years the number of animals with adolescent live weight measures has greatly increased, and over 200,000 animals born in 2017 were weighed as adolescents (Figure 2). Adolescent live weights share a strong positive genetic correlation with live weight during first lactation (Section 4), suggesting that adolescent live weight phenotypes are an accurate predictor trait for live weight EBVs.

In Ireland, adolescent live weight data are included as predictor phenotypes for the live weight EBV using a nine trait, multi-variate analysis (Evans et al., 2014). Adolescent live weights at different ages are considered genetically correlated but distinct traits. In the Irish cattle population, genetic correlations between live weights measured across ages range from 0.29 to 0.70. The Irish analysis also makes use of live weight phenotypes collected during lactation. These lactation live weights are considered to be repeated measures of a ‘cow live weight’ trait. Accordingly, live weight during lactation is one of the nine traits considered in the multivariate analysis. The national genetic evaluation system in NZ produces EBVs for mature live weight using a univariate repeated measures analysis. Lactation phenotypes are the single predictor phenotype,

and live weight phenotypes obtained across multiple lactations are treated as repeated measures of the same trait (Holmes et al., 2003). The treatment of live weight phenotypes measured across lactations is similar in Irish and NZ live weight genetic evaluations, as both countries consider live weight measures from any lactation to be the same trait. The two countries differ in their treatment of adolescent live weights, as these phenotypes are not currently used as a predictor for the mature live weight EBV in NZ. The genetic covariances between adolescent live weights and live weight during lactation in the NZ Holstein-Friesian population (Section 4) are higher than those observed in Irish cattle (Evans et al., 2014). The higher genetic covariances observed in NZ cattle may mean the multi-variate approach taken in Ireland is not optimal for NZ.

A univariate, repeated measures model is appropriate where longitudinal observations have heterogeneity of variance, and genetic correlations are 1. Our previous analysis indicated that the genetic correlations between live weights across ages are close to 1 (0.79-0.97; Section 4), however, the variance of live weight increases as animals grow. Taken together, these two characteristics indicate that phenotypes obtained across multiple age classes can be combined into a univariate repeated measures analysis, but that they must be standardised for variance. We hypothesised that the inclusion of adolescent live weight phenotypes as predictors of a FLW EBV would improve the accuracy of the EBV, compared to using FLW phenotypes alone.

5.3. Materials and Methods

This study involved a comparison of the accuracy of EBVs generated by two analyses. In the first analysis, we produced EBVs using only phenotypes measured during first lactation. In the second analysis, we produced EBVs using live weight phenotypes measured from adolescence through to first lactation. We established two forms of the generalised linear mixed model to produce these EBVs. The first was a univariate mixed model, where animals had a maximum of one phenotype, measured during first lactation. The second was a repeated measure mixed model, where animals could have multiple phenotypes, measured at varying ages. We determined the validity of these

models using a number of standard validation techniques. We defined the accuracy of the EBVs as the correlation between EBVs produced, and live weight phenotypes from first lactation that were specifically omitted from the analysis. By omitting certain phenotypes, we were able to produce parent average EBVs for animals whose FLW phenotype was known. The accuracy of these parent average EBVs could then be established as the correlation between the EBVs and the omitted phenotype. In the case of the second analysis (repeated measure), EBVs were produced and tested under two further scenarios. Scenario two showed the accuracy of EBVs where the animal's dam had an adolescent phenotype (while the animal itself had no phenotypes measured in its own right, or for its progeny) Scenario three showed the accuracy of EBVs where the animal had an adolescent live weight included in the analysis.

5.3.1. Analysis 1: Univariate Mixed Model

5.3.1.1. Univariate Mixed Model

A linear mixed model was established to complete a univariate analysis. The matrix representation of the linear mixed model equation is:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \qquad \text{Equation } 4_1$$

where **y** is a vector of phenotypes for the FLW category, **b** is a vector of fixed effects for the FLW category, **u** is a vector of breeding values (random effects) for the FLW category. The vector **e** is a vector of residuals corresponding to each of the observations in the FLW category. **X** is an incidence matrix relating each phenotype record in the FLW category to the relevant fixed effects. **Z** is an incidence matrix relating phenotypes to their corresponding breeding value, with a row for each phenotype and a column for each animal represented in **u**. For a full description of this model, including location and dispersion parameters, see Section 9.2.

[1] Equation 4 is similar to Equation 3. The difference being that this analysis included live weights from the first lactation weight age category only.

5.3.1.2. Fixed Effects

Fixed effects were as described in Section 4.3.6.

5.3.2. Analysis 2: Repeated Measure Mixed Model

5.3.2.1. Homogeneity of Variance Adjustment

A condition of a simple repeated measures analysis is homogeneity of variance across phenotypes. Previously we showed that the variance of live weight data increases with the mean (Figure 3), and so as animals grow, variance increases. To satisfy the condition of homogeneity of variance we standardised the live weight phenotypes for variance. First, we categorised the phenotypes based on the animal's age when it was weighed and then we adjusted each phenotype for relevant fixed effects. For the age categories WW, PW and YW, these fixed effects were 'age in days' (see Section 4.3.6.2) and contemporary group (see Section 4.3.6.1). For the FLW age category, lactation day (see Section 4.3.6.3) was included as a third fixed effect. As a final step, we divided each adjusted phenotype by the mean variance of the phenotypes in the relevant age category. This process is further detailed in Section 9.4.

5.3.2.2. Repeated Measure Mixed Model

The model equation for the repeated measures model was as follows:

$$\boldsymbol{y}_{\mathbf{adj\_dev}} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wh} + \mathbf{e} \qquad \text{Equation 5}$$

Where $\boldsymbol{y}_{\mathbf{adj\_dev}}$ is a vector of variance adjusted live weight deviations (see Section 9.4). $\mathbf{b}$ is a vector of fixed effects, $\mathbf{u}$ is a vector of breeding values (random effects) and $\mathbf{e}$ is a vector of residuals corresponding to each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$. $\mathbf{h}$ is a vector of permanent environment effects, accounting for residual covariance between repeated observations for the same animal. $\mathbf{X}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to the relevant fixed effects. $\mathbf{Z}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to the corresponding breeding value, with a column for each animal represented in $\mathbf{u}$. $\mathbf{W}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to each unique animal with an observation.

Linear equations were solved using the Gauss-Seidel method. The Gauss-Seidel method requires knowledge of the variance parameters. A single site Gibbs sampler, using a Markov-chain Monte Carlo (MCMC) technique was used to obtain samples of the variance components required to build the repeated measures mixed model equations. The posterior means of samples of the genetic (σ_g^2), permanent environment (σ_h^2) and residual (σ_r^2) variances were 0.42, 0.42 and 0.25, respectively. These posterior means were used as the assumed variance components. For a full model description, including location and dispersion parameters see Section 9.3. To view the MCMC samples results see Section 9.7.

5.3.2.3. Fixed Effects

Phenotypes were preadjusted for a number of fixed effects as a part of the variance adjustment process (see Section 5.3.2.1). Contemporary group (see Section 4.3.6.1) was included again as a fixed effect in the repeated measures analysis. The inclusion for contemporary group as a fixed effect in both analyses allowed degrees of freedom across observations to be defined appropriately.

5.3.3. Software

Command line bash scripts were generated to pre-process phenotypic and pedigree data. Genetic analysis and post-processing were performed using the statistical software Julia (*The Julia Language*, 2019) The package add-on JWAS (Cheng, 2019) was used for genetic analysis. The post-processing of results was carried out using the packages CSV, Statistics, LinearAlgebra, StatsPlots, DataFrames, DelimitedFiles, Distributions, Measures. See Section 11 for scripts.

5.3.4. Solver

Linear equations were solved using the Gauss-Seidel method. A single site Gibbs sampler, using a MCMC technique was used to obtain samples of the variance components required to build the repeated measures mixed model equations (see Section 5.3.2.2).

5.3.5. Data

Pedigree and phenotype data for approximately 1.3 million animals were provided by DairyNZ in June 2018. Various filtering steps were applied (Section 9.1.1), resulting in a final count of approximately 515,000 animals across all age categories.

5.3.6. Model Validation

A forward cross validation (Legarra & Reverter, 2017) was undertaken for both analyses using a subset of females born in 2015. The phenotypes of these animals were omitted and each analysis was re-run using partial data. The $EBVs_{(partial)}$ were then compared to $EBV_{(whole)}$ to produce general validation statistics for each model. These general validation statistics were obtained for each of the five analysis described in this chapter (appendix 10). Following general validation, the predictive ability of the univariate (FLW) and the repeated measures analyses were established under a number of test scenarios (Section 5.3.7).

5.3.6.1. Selecting Validation Animals

Females born in 2015 were used for validation because this age group was old enough to have phenotypes for all age categories (WW, PW, YW, FLW). Adolescent phenotypes (weights obtained between 181 and 480 days old) were collected in 2015 and 2016. First lactation phenotypes (weights obtained when animals were 791 to 940 days old) were collected in 2017. There were between 30,000 and 45,000 validation animals for each adolescent age category, representing around 250 sires. There were fewer validation animals in the FLW age category, but sire representation remained high, with 147 sires represented across 5,126 daughters (Table 7).

5.3.6.2. Validation Statistics

A number of validation statistics were produced to assess the bias, dispersion and accuracy of each model. The following equations describe the validation statistics, where $\hat{\mathbf{u}}_{\text{whole}}$ is a vector of EBVs produced by the main evaluation, where all eligible phenotypes are included. $\hat{\mathbf{u}}_{(\text{partial})}$ is a vector of EBVs

produced by the validation evaluation where the phenotypes of 2015 born animals were excluded. All validation statistics include 2015 born animals only.

Table 7 Count of validation animals and the number of sires represented for each analysis.

Analysis	Count of validation animals	Count of sires*
Univariate: WW	45,114	286
Univariate: PW	30,900	225
Univariate: YW	36,839	243
Univariate: FLW	5,126	147
Repeated Measures: WW, PW, YW, FLW	67,328	448

* = Count of sires included those with at least 10 daughters with live weight observations within the relevant age category.

5.3.6.2.1. Mean Bias

In an unbiased evaluation, the estimate of the intercept b_0 should equal 0 (Equation 6; Legarra & Reverter, 2018).

$$b_0 = E(\hat{\mathbf{u}}_{whole} - \hat{\mathbf{u}}_{partial}) \qquad \text{Equation 6}$$

5.3.6.2.2. Change in Dispersion

It is a property of best linear unbiased prediction (BLUP) that the $Cov(\hat{\mathbf{u}}_{\mathbf{whole}}, \hat{\mathbf{u}}_{\mathbf{partial}})$ is equal to the $Var(\hat{\mathbf{u}}_{\mathbf{whole}})$ (Equation 7). It follows that b_1 should be 1 (Legarra & Reverter, 2018). An estimate of b_1 of greater than or less than 1 indicates that the EBVs(partial) were either under or over dispersed, respectively.

$$b_1 = \frac{Cov(\hat{\mathbf{u}}_{whole}, \hat{\mathbf{u}}_{\mathbf{partial}})}{Var(\hat{\mathbf{u}}_{\mathbf{whole}})} \qquad \text{Equation 7}$$

5.3.6.2.3. Population Accuracy

The r value indicates the degree of re-ranking between the EBVs(partial) and EBVs(whole) (Equation 8). As more data are added, EBVs become closer to the true breeding values. A higher correlation is optimal, as this shows that the accuracy of $\hat{\mathbf{u}}_{\mathbf{partial}}$ is similar to $\hat{\mathbf{u}}_{\mathbf{whole}}$.

$$r_{\hat{\mathbf{u}}_{\mathbf{whole}},\hat{\mathbf{u}}_{\mathbf{partial}}} = \frac{\mathrm{Cov}(\hat{\mathbf{u}}_{\mathbf{whole}}, \hat{\mathbf{u}}_{\mathbf{partial}})}{\sqrt{\mathrm{Var}(\hat{\mathbf{u}}_{\mathbf{whole}})\mathrm{Var}(\hat{\mathbf{u}}_{\mathbf{partial}})}}$$ Equation 8

5.3.7. Predictive Ability

Various phenotype data were excluded from both the FLW analysis and the repeated measures analysis (Table 8). These data exclusions test each analysis by simulating situations where forward prediction of EBVs are required. The FLW phenotypes of animals were omitted in every test. The correlation between the omitted FLW phenotypes, and the EBVs produced was used as a metric to assess the predictive ability of a model within each test scenario.

Table 8 Parameters for each test scenario.

	Live weight phenotypes included		**Criteria for animals included in the correlation**	**Count of validation animals**	**Count of validation sires***
	2015 born	**Other**			
Analysis 1 Scenario 1	**none**	**FLW**	- 2015 born - Have FLW phenotype	5,955	198
Analysis 2 Scenario 1	**none**	**WW PW YW FLW**	- 2015 born - Have FLW phenotype	5,955	198
Analysis 2 Scenario 2	**none**	**WW PW YW FLW**	- 2015 born - Have FLW phenotype - Dams have at least one live weight phenotype	1,297	23
Analysis 2 Scenario 3	**WW PW YW**	**WW PW YW FLW**	- 2015 born - Have FLW phenotype - Have at least one adolescent live weight phenotype	1,764	52

Note. * = Count of sires included those with at least 10 daughters with live weight observations within the relevant age category. Analysis 1 = FLW

Univariate analysis. Analysis 2 = Repeated measures univariate analysis including adolescent live weight phenotypes.

5.4. Results

5.4.1. Analysis 1: First Lactation Weight (FLW) Univariate Analysis

The FLW univariate analysis included 147,000 animals, representing around 3,400 sires. The integrity of the model was validated using standard validation procedures (see Section 10 for validation results).

5.4.1.1. Scenario One

The phenotypes of all 2015 born animals were excluded from the analysis. These animals remained in the pedigree, so their EBVs were produced. These EBVs were forward predictions, based on the average of the animal's parents. The correlation between these parent average EBVs, and the omitted FLW phenotypes of these animals was 0.27. This result indicates that the live weight EBVs for these animals are able to explain 7% of the variance in their FLW live weight phenotypes.

5.4.2. Analysis 2: Repeated Measures Analysis

The repeated measures analysis included phenotypes for 515,500 animals, representing 4,500 sires. As with the FLW univariate model, standard validation procedures were followed (see Section 10 for validation results).

5.4.2.1. Scenario One

The WW, PW, YW and FLW phenotypes of all 2015 born animals were excluded from the analysis. These animals remained in the pedigree file, and so their EBVs were obtained for these animals. The correlation between the parent average EBVs and the FLW phenotype for these 5,955 animals was 0.28. This result indicates that the live weight EBVs for these animals are able to explain 8% of the variance in their FLW live weight phenotypes.

5.4.2.2. Scenario Two

The WW, PW, YW and FLW phenotypes of all 2015 born animals were excluded from the analysis. These animals remained in the pedigree file, and

so their EBVs were obtained. There were 5,955 animals with omitted FLW data. This group was further reduced, based on whether the dam of an animal had a phenotype record. Around 1,700 animals had an FLW phenotype (omitted) and a dam with a phenotype included in the analysis. The correlation between the parent average EBVs for these animals and their FLW phenotypes was 0.34. This result indicates that when a dam has a phenotype record, the EBVs for her progeny will explain around 11.5% of the variation in the progeny's subsequent FLW phenotypes.

5.4.2.3. Scenario Three

The FLW phenotypes of the 2015 born animals were excluded. Of the 2015 born animals with a FLW weight phenotypes, around 1,200 animals also had WW, PW or YW phenotypes. These WW, PW and YW phenotypes were included in the analysis. The correlation between EBVs and the omitted FLW phenotypes was 0.59. The EBVs produced in this analysis were able to explain around 30% of the variance in the subsequent FLW phenotype for these validation animals.

The results of these three repeated measures scenarios indicate that including adolescent live weight as a predictor phenotype will improve the accuracy of EBVs for animals with adolescent weights recorded, and their progeny.

5.5. Discussion

5.5.1. Research Summary

The aim of this study was to demonstrate the utility of adolescent live weight in predicting first lactation live weight (FLW) EBVs. To address this objective, we established the predictive ability of EBVs produced both with and without adolescent live weights.

We omitted the FLW phenotypes for a subset of animals (those born in 2015) from each analysis. This omission allowed for the calculation of the correlation between the EBVs generated for these animals using only their ancestral information and individual adolescent weights, with their subsequently observed FLW phenotype deviations. Our results suggest that when a cow has an

adolescent live weight phenotype, this observation greatly improves the predictive ability of her live weight EBV. EBVs produced using at least one adolescent live weight observation explained around 30% of the variation in live weight during first lactation. By contrast, when all adolescent live weights were excluded from the analysis (i.e. the FLW univariate analysis), the proportion of variance in FLW explained by the EBV dropped to 7%. Including adolescent live weight phenotypes did not generally improve the predictive ability of EBVs for an animal when her own adolescent observation was still excluded from the analysis. The exceptions were animals whose dam had an adolescent live weight included in the analysis. If an animal's dam had an adolescent phenotype the proportion of variation in FLW explained by the parent average EBV increased from 8% to 11.5%. Taken together, these findings suggest that adolescent live weights are a useful predictor phenotype for live weight EBVs, when sufficient adolescent data exist.

5.5.2. Research Limitations

A univariate analysis, including only FLW phenotypes was used to represent the current national genetic evaluation system for live weight. A FLW univariate analysis will not be entirely representative of the current national system, as live weight EBVs published for dairy cattle in NZ incorporate phenotypes from all lactations. That said, EBVs produced using a univariate FLW analysis should provide a close approximation as relatively few animals have live weight records in subsequent lactations (Section 3). This is especially relevant regarding EBVs for bulls, as most daughter phenotypes are measured when daughters are in their first lactation.

The data filtering process involved removing repeated live weight measures for an same animal within an age category. For example, if an animal was weighed twice within the weaning weight category, only one of these weights was included in our analysis. If an animal had a live weight measure in two categories, both of these phenotypes were included in the repeated measures analysis. This filtering approach is inconsistent, and including these repeated measures within categories may improve the accuracy of EBVs.

The process we used to standardise the live weight phenotypes for variance required multiple analyses and was logistically complex. Live weight phenotypes were categorised based on the age of the animals when they were weighed, adjusted for fixed effects, and then standardised for variance. These adjusted, standardised phenotypes were then combined into a repeated measures analysis. While this process was satisfactory for addressing our research question, there are several alternatives that would be simple. One example of a simpler approach would be to scale the phenotypes to a common variance by adjusting the values in the **Z** matrix (Equation 5). **Z** is a matrix of zeros and ones, and it relates each phenotype to relevant breeding values. The values in the **Z** matrix can be replaced with values that are greater than or less than one, in order to scale the associated phenotype up or down. A second example would be to use a multi-variate approach. Our ability to undertake a multi-variate analysis was limited by the number of animals represented across all age categories, and possibly the structure of the genetic (co)variance matrix between age categories. This study included a total of 515,475 animals across the four age categories (WW, PW, YW, FLW). These data were extremely unbalanced. There were around 80,000 animals weighed within all WW, PW and YW categories, but only 1,700 of these animals were also weighed during first lactation. In addition to the lack of representation across age categories, the genetic correlations between traits were approaching unity. If the genetic correlations between traits are 1, then the genetic (co)variance matrix required for the multi-variate analysis will not be positive definite. Non positive definite (co)variance matrices will render the equations un-solvable. As the genetic variances approach this boundary, the analysis will experience convergence problems, or in a Bayesian context there will be mixing problems that manifest as a lack of convergence of functions of the samples from the Markov chain. A robust multi-trait analysis, across all four age categories was not achievable with the current data. Going forward, a multi-variate approach may become viable if representation of animals across all age categories improves.

This study did not use live weight records obtained during lactation from automated measuring devices (known as ‘walk over weigh’ [WOW]). WOW systems typically weigh animals as they leave milking. High frequency live

weight information offers a management benefit that is not obtained from one-off weighing, as week to week variation in live weight can be used to monitor animal health. WOW phenotypes have the potential to strengthen this research, as these weighing systems make it relatively trivial to gain live weight data on cows during lactation. Incorporating WOW data could provide a long-term solution for increasing the representation of animals across lactation live weight categories because farmers may decide that the management benefits justify the initial installation investment. It is worth noting that even if WOW facilities become commonplace, adolescent live weight data will still be high value predictor trait as it can be measured early in an animal's life thus reducing the generation interval.

An EBV is an estimation of how the animal's genetic merit will manifest as a phenotype across a range of environments. Phenotypes are used to predict EBVs, but a phenotype is the product of both the animal's genetic merit, and the specific environment to which the animal is exposed. The effect of the environment will not be repeatable if the environment is changed. Therefore, when predicting an EBV it is important to separate the effect of the animal's genetic merit from the effect of environment. The process of separating genetics from environment is relatively trivial for bulls, as they often have hundreds of daughters across many herds. By contrast, cows rarely have multiple offspring and they themselves do not usually change environment (i.e. location). The lack of representation across environments is somewhat mitigated by the use of the animal model, as the phenotypes from related cows are observed in different environments. A key finding of this research is that incorporating adolescent live weights into the genetic evaluation of live weight improved the proportion of FLW variance explained by the live weight EBV. It is possible that the improved correlations that we see between FLW EBVs predicted from adolescent weights and subsequent FLW phenotypes could be inflated because the environmental effects that cause adolescent weights to deviate from parent average may also cause FLW weights to deviate from parent average.

5.5.3. Practical Implications

The true breeding value (TBV) of an animal is not known, but it can be estimated. The accuracy of an individual animal's EBV will be determined by the accuracy of its parent's EBVs and information that can be inferred about the Mendelian sampling of the animal itself. Mendelian sampling occurs at random, and the effect on an animal's performance can be either positive or negative. The genetic merit of an animal can be estimated with high accuracy using progeny information, provided there are a reasonable number of progeny across multiple environments. In the absence of offspring information, we can only estimate the effect of Mendelian sampling by measuring an appropriate predictor phenotype on the animal itself.

In the NZ dairy industry, EBVs for bulls are often estimated using phenotype measures on female progeny. The genetic control and thus expression of a trait can be sexually dimorphic, but it is the female expression of the trait that is of primary interest in the dairy industry. The EBVs for cows are predicted using their parent average, their own phenotypic measures, and those from their female progeny. As a bull or cow gains phenotype data—either directly or through daughters—this information will gradually increase the accuracy of their EBV.

The value of phenotype information depends on the number of animals contributing data. All relevant phenotype data will increase EBV accuracy, however, data from multiple animals is optimal for two reasons. First, separating the effect of the environment and genetic merit is more accurate if the genetic merit can be observed across multiple environments. Second, the genetic merit of an animal's progeny will also be influenced by Mendelian sampling. If there are too few progeny, the average effect of Mendelian sampling may deviate from zero.

Including adolescent live weight data will greatly increase the phenotype data available to predict live weight EBVs. Of the animals born each year, around 30,000 (or 3%) will go on to have a live weight phenotype recorded during lactation. If adolescent live weights are included, the number of phenotyped

animals will lift to around 300,000, or 30%. The accuracy of live weight EBVs will immediately increase for animals with adolescent live weight phenotypes. This lift in EBV accuracy likely reflects the value of these adolescent data as an indicator of the Mendelian sampling effect on an animal's genetic merit.

The increase in accuracy will also be realised through more accurate live weight EBVs for the parents of females with adolescent phenotypes. These adolescent data will be especially valuable for sires. Sires involved in formal progeny testing would eventually gain sufficient daughter FLW phenotypes, but adolescent live weight phenotypes will be obtained earlier in life. EBV accuracy earlier in life will allow earlier genetic selection for the live weight trait. Earlier selection can shorten the generation interval, and thus increase the rate of genetic gain. Sires that are not involved in formal progeny testing will perhaps gain the most benefit from the inclusion of adolescent data. These bulls will have a greater opportunity to obtain daughter live weight phenotypes. Therefore, the accuracy of selection among these bulls will improve.

6. Main Summary

The hypotheses of our research were two-fold. The first was that the genetic correlations between live weight across ages would be strong and positive in a population of New Zealand Holstein-Friesian Cattle. The results of study one (Section 4) support this hypothesis, in that we observed genetic correlations ranging for 0.79 to 0.96. Our second hypothesis was that adolescent live weight would add value as a predictor phenotype for the live weight EBV. The results of study two (Section 5) support this hypothesis in that when animals had an adolescent live weight included in the analysis, EBVs were able to explain around 30% of the variance in subsequent live weight during first lactation.

The value of including adolescent live weight phenotypes is likely to become more pronounced as a greater proportion of females are weighed through adolescence. Going forward, we expect that greater attention to young stock growth will lead to greater volumes of adolescent live weight data being available for national genetic evaluation.

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8. Index

Adolescent Live Weight: Live weight phenotypes obtained prior to an animals first lactation (when an animal is less than two years old).

Breeding Worth (BW): The national selection index for New Zealand dairy cattle. Breeding Worth provides an estimation of the value of an animal's genetic merit, based on estimated breeding values for eight traits (Milk Fat, Milk Protein, Milk Litres, Somatic Cell Score, Live Weight, Fertility, Residual Survival, Body Condition Score).

Estimated Breeding Value (EBV): An estimation of an animal's genetic merit for a given trait.

First Lactation Weight (FLW): Live weights obtained when an animal is between 791 days and 940 days.

Mature Live Weight: Live weight phenotypes obtained when an animal is at least six years old.

Milk Solids: Milk Fat (kgs) and Milk Protein (kgs).

Progeny Testing Scheme: A co-ordinated phenotype collection initiative, designed to generate daughter phenotypes for targeted sires. These schemes ensure that the sires involved have sufficient daughter phenotype information across a range of relevant traits to enable robust genetic evaluation.

Puberty Weight (PW): Live weights obtained when an animal is between 281 and 380 day old.

Weaning Weight (WW): Live weights obtained when an animal is between 181 and 280 day old.

Yearling Weight (YW): Live weights obtained when an animal is between 381 and 480 day old.

9. Appendices

9.1. Data Filtering

9.1.1. Data Exclusions

A total of 12,986,697 live weight records were received representing 1,385,320 animals. A number of exclusions were carried out before further analyses were performed.

9.1.1.1. Sex

Analysis include phenotype data from females only

9.1.1.2. Breed Proportions

The analysis was restricted to animals that were predominantly Friesian and/or Holstein. In DIGAD, the breed of an animal is described in breed proportions, expressed in sixteen parts. No distinction was made in these analyses between Holstein and Friesian animals. That is, animals were classified as Holstein-Friesian when at least fourteen of sixteen breed parts were Holstein or Friesian. This edit resulted in a total of 3,283,040 weight records available for Holstein-Friesian females, these records originating from 1,006,099 individuals.

9.1.1.3. Categorising Weight Phenotypes Based on Animal Age

Four age categories were created based on the age of the animal when it was weighed (Table 9). Weights that fell outside of these age ranges were disregarded.

Table 9 Count of Holstein-Friesian females with a live weight phenotype within each age category.

Trait	Age range (days)	Count of females with weight record
Weaning Weight (WW)	181 - 280	309,044
Puberty Weight (PW)	281 - 380	220,743
Yearling Weight (YW)	381 - 480	220,479
Post-Calving Weight (FLW)	791 - 940	220,874

9.1.1.4. Outlier Observations

Phenotypes that were greater than three standard deviations from the mean of the relevant contemporary group were excluded (Table 10).

Table 10 Count of Holstein-Friesian females within each age category, after outlier phenotypes are excluded

Age category	Animal count before exclusion	Animal count after exclusion
WW	309,044	289,551
PW	220,743	202,533
YW	220,479	203,374
FLW	220,874	213,330

9.1.1.5. Small Contemporary Groups

Phenotypes for animals from contemporary groups with fewer than 10 animals were excluded (Table 11).

Table 11 Count of Holstein-Friesian females within each age category, after small contemporary groups have been removed.

Age category	Animal count before exclusion	Animal count after exclusion
WW	289,551	272,178
PW	202,533	185,198
YW	203,374	191,346
FLW	213,330	197,045

9.1.1.6. Historic Data

Phenotypes from animals born prior to 1995 were excluded (Table 12).

Table 12 Count of Holstein-Friesian females within each age category, after animals born prior to 1995 have been removed.

Age category	Animal count before exclusion	Animal count after exclusion
WW	272,178	271,794
PW	185,198	185,101
YW	191,346	191,109
FLW	197,045	147,450

9.1.1.7. Animals Without a Two-Year-Old Calving (FLW category only)

Phenotypes for animals who did not calve when they were two-years-old were excluded from the FLW category (Table 13).

Table 13 Count of Holstein-Friesian females within the 'first lactation weight' (FLW) age category, after animals without a two-year-old calving have been removed.

Age category	Animal count before exclusion	Animal count after exclusion
FLW	147,450	146,444

9.1.2. Animal Numbers in Univariate Analysis

There were between 140,000 and 270,000 animals included in each analysis. There were approximately 1000 sires represented in each of the adolescent age categories (WW, PW and YW). Around 3400 sires were represented in the FLW category (Table 14).

Table 14 Number of animals represented in each univariate analysis following data edits

Age category	Count of animals	Number of sires*	Number of contemporary groups
WW	271,794	1,381	9,164
PW	185,101	992	6,270
YW	191,109	993	6,018
FLW	146,444	3,416	4,204

Note. * = Number of sires represented by at least 10 daughters. A disproportionately large number of sires are represented in the FLW category, as the majority of these live weight phenotypes are generated within progeny testing schemes. Progeny testing schemes are designed to generate phenotypes for a large number of candidate sires.

9.1.3. Animal Numbers in Bivariate Analysis

To be eligible for a bivariate analysis, either the animal, or at least one member of the animal's contemporary group must have phenotypes in both age categories (Table 15).

Table 15 Number of animals represented in each bivariate analysis following data edits.

Model	Count of animals with weights in both age categories*	Number of sires**	Number of contemporary groups
WW with PW	109,237 (165,784)	689	WW: 5,100 PW: 4,539
WW with YW	103,530 (160,847)	640	WW: 4,782 YW: 4,213
WW with FLW	4,688 (9,933)	89	WW: 235 FLW: 195
PW with YW	96,769 (141,654)	633	PW: 4,158 YW: 3,983
PW with FLW	3,034 (7,212)	51	PW: 185 FLW: 158
YW with FLW	3,978 (7,452)	74	YW: 203 FLW: 166

Note. * = Brackets show the total number of animals included in each bivariate analysis. Animals weighed in only one of the two age categories were included if at least one other animal in their contemporary group had a phenotype in both age categories. ** = Number of sires included those represented by at least 10 daughters.

9.1.4. Animal Numbers in Repeated Measure Analysis

Animals were included in the repeated measures analysis if they had a weight in at least one age category.

Table 16 Number of animals represented in each repeated measures analysis following data edits.

Model	Count of animals with a live weight in at least 1 age category	Number of sires*	Number of contemporary groups
Repeated Measures	515,476	4,539	24,278

* = Number of sires included those represented by at least 10 daughters.

9.2. Univariate and Bivariate Mixed Model Description

9.2.1. Model Equation

A general linear mixed model was established to complete univariate and bivariate analyses. The matrix representation of the general linear mixed model is:

$$\mathbf{y_i} = \mathbf{X_i b_i} + \mathbf{Z_i u_i} + \mathbf{e_i} \qquad \text{Equation 3}$$

where $\mathbf{y_i}$ is a vector of phenotypes for the i_{th} age category (WW, PW, YW, FLW), $\mathbf{b_i}$ is a vector of fixed effects for the i_{th} age category, $\mathbf{u_i}$ is a vector of breeding values (random effects) for the i_{th} age category. The vector $\mathbf{e_i}$ is a vector of residuals corresponding to each of the observations in the i_{th} age category. $\mathbf{X_i}$ is an incidence matrix relating each phenotype record in the i_{th} age category to the relevant fixed effects. $\mathbf{Z_i}$ is an incidence matrix relating phenotypes to their corresponding breeding value, with a row for each phenotype in the i_{th} age category and a column for each animal represented in $\mathbf{u_i}$.

9.2.2. Location Parameter Assumptions

The expected i_{th} age category phenotype for an animal chosen at random is the mean of its contemporary group, adjusted for the applicable fixed covariates.

$$\mathrm{E}[\mathbf{y_i}] = \mathbf{X_i b_i}$$

The expected values of $\mathbf{u_i}$ and $\mathbf{e_i}$ for an animal chosen at random are 0.

$$\mathrm{E}[\mathbf{u_i}] = \mathbf{0}$$

$$\mathrm{E}[\mathbf{e_i}] = \mathbf{0}$$

9.2.3. Dispersion Parameter Assumptions

9.2.3.1. Genetic Variance/Covariance

The variance of $\mathbf{u_i}$ is equal to the numerator relationship matrix multiplied by the genetic variance.

$$\mathrm{Var}[\mathbf{u_i}] = \mathrm{G} = \mathbf{A}\sigma^2_{g(i)}$$

where **A** is the numerator relationship matrix and $\sigma_{g(i)2}$ is the additive genetic variance for the i_{th} age category. The diagonals of **A** are 1 plus the inbreeding coefficients of each animal, and the off diagonals of **A** represent the pairwise pedigree relationships between corresponding animals. The breeding values of animals are correlated according to their pedigree relationships. The off-diagonals of $\mathbf{A}\sigma_{g(i)2}$ are the pairwise covariances between the breeding values of corresponding animals for the i_{th} age category.

This variance structure assumes the following:

- Genotype by environment interactions are not present.
- Non-additive genetic effects are not relevant.

9.2.3.2. Residual Variance/Covariance

The variance of $\mathbf{e_i}$ is the residual variance.

$$\mathrm{Var}[\mathbf{e_i}] = \mathrm{R} = \mathbf{I}\sigma^2_{e(i)}$$

where **I** is an identity matrix with one column and one row for every animal with a phenotypic record, and $\sigma_{e(i)2}$ is the residual variance for the i_{th} age category.

This variance structure assumes the following:

- (Co)variances between residuals are zero.
- Homogeneity of residual variance exists.
- The vector of residuals **(e)** has a normal distribution.

9.2.3.3. Covariance Between Genetic Effects and Residuals

Breeding values and residuals for the ith age category are assumed to be uncorrelated.

$$\mathrm{Cov}[\mathbf{u_i}, \mathbf{e_i}] = \mathbf{0}$$

9.2.3.4. Phenotypic Variance

The phenotypic variance of the ith age category is the sum of the genetic and residual variance for the ith age category.

$$\mathrm{Var}[\mathbf{y_i}] = \mathbf{Z_i}\mathrm{G_i}\mathbf{Z_i'} + \mathbf{R_i}$$

9.3. Repeated Measures Model Description

9.3.1. Model Equation

A general linear mixed model was established to complete a repeated measure analyses. The matrix representation of the general linear mixed model is:

$$\boldsymbol{y}_{\mathbf{adj\_dev}} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{Wh} + \mathbf{e} \qquad \text{Equation 5}$$

Where $\boldsymbol{y}_{\mathbf{adj\_dev}}$ is a vector of variance adjusted live weight deviations (see Section 9.4). $\mathbf{b}$ is a vector of fixed effects, $\mathbf{u}$ is a vector of breeding values (random effects) and $\mathbf{e}$ is a vector of residuals corresponding to each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$. $\mathbf{h}$ is a vector of permanent environment effects, accounting for residual covariance between repeated observations for the same animal. $\mathbf{X}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to the relevant fixed effects. $\mathbf{Z}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to the corresponding breeding value, with a column for each animal represented in $\mathbf{u}$. $\mathbf{W}$ is an incidence matrix relating each row of $\boldsymbol{y}_{\mathbf{adj\_dev}}$ to each unique animal with an observation.

9.3.2. Location Parameter Assumptions

The expected phenotype for an animal chosen at random is the mean of its contemporary group, adjusted for the applicable fixed covariates.

$$\mathrm{E}[\mathbf{y}] = \mathbf{Xb}$$

The expected values of **u** and **e** for an animal chosen at random are 0.

$$\mathrm{E}[\mathbf{u}] = \mathbf{0}$$

$$\mathrm{E}[\mathbf{e}] = \mathbf{0}$$

9.3.3. Dispersion Parameters

9.3.3.1. Genetic Variance

The variance of **u** is equal to the numerator relationship matrix multiplied by the genetic variance.

$$\mathrm{Var}[\mathbf{u}] = \mathrm{G} = \mathbf{A}\sigma_{\mathrm{g}}^2$$

where **A** is the numerator relationship matrix and σ_{g2} is the additive genetic variance. The diagonals of **A** are 1 plus the inbreeding coefficients of each animal, and the off diagonals of **A** represent the pairwise pedigree relationships between corresponding animals. The breeding values of animals are correlated according to their pedigree relationships. The off-diagonals of $\mathbf{A}\sigma_{g2}$ are the pairwise covariances between the breeding values of corresponding animals.

This variance structure assumes the following:

- Genotype by environment interactions are not present.
- Non-additive genetic effects are not relevant.

9.3.3.2. Permanent Environmental Variance

The variance of $\mathbf{h}$ is the permanent environmental variance.

$$\mathrm{Var}[\mathbf{h}] = \mathbf{H} = \mathbf{I}\sigma_{\mathrm{h}}^2$$

where **I** is an identity matrix with one column and one row for every animal with a phenotypic record, and σ_{h2} is the permanent environmental variance.

This variance structure assumes the following:

- Co-variances between residuals are zero.
- Homogeneity of residual variance exists.
- The vector of residuals **[h]** has a normal distribution.

9.3.3.3. Residual Variance

The variance of **e** is the residual variance.

$$\mathrm{Var}[\mathbf{e}] = \mathbf{R} = \mathbf{I}\sigma^2_{e(i)}$$

where **I** is an identity matrix with one column and one row for every animal with a phenotypic record, and $\sigma_{e(i)2}$ is the residual variance for the i_{th} age category.

This variance structure assumes the following:

- Co-variances between residuals are zero.
- Homogeneity of residual variance exists.
- The vector of residuals **(e)** has a normal distribution.

9.3.3.4. Phenotypic Variance

The phenotypic variance is the sum of the genetic, permanent environment and residual variance.

$$\mathrm{Var}[\mathbf{y}] = \mathbf{ZGZ'} + \mathbf{WHW'} + \mathbf{R}$$

Where **Z** is an incidence matrix relating each phenotype to an EBV.

9.4. Standardising Variance

Phenotypes were categorised into four groups, based on the age of the animal when it was weighed. These groups were as follows: 181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days

to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW). Four univariate analyses were then carried out (see Section 9.2 for model description), and the phenotypes contributing to each age category were adjusted for relevant fixed effects (Equation 9).

$$\mathbf{y_{dev(i)}} = \mathbf{y_i} - \mathbf{X_i b_i} \qquad \text{Equation 9}$$

where $\mathbf{y_i}$ is a vector of observations for the ith age category, $\mathbf{b_i}$ is a vector of fixed effects for the ith age category and $\mathbf{X_i}$ is an incidence matrix relating each phenotype record in the ith age category to the fixed effects.

These adjusted phenotypes ($\mathbf{y_{dev(i)}}$) were then standardised for variance (Equation 10)

$$\mathbf{y_{std\_dev(i)}} = {}^{\mathbf{y_{dev(i)}}}/_{\sigma_{\mathbf{y_{dev(i)}}}} \qquad \text{Equation 10}$$

Table 17 shows the variance of $\mathbf{y_{dev(i)}}$ (Equation 9) and the variance of $\mathbf{y_{std\_dev(i)}}$ (Equation 10) for each age category (WW, PW, YW, FLW). The variance of $\sigma_{y_{std\_dev}}$ is exactly 1 across all age categories (Table 17).

Table 17 Standard deviation of each age category before and after adjusting for variance

Age category	$\boldsymbol{\sigma_{y_{dev}}}$	$\boldsymbol{\sigma_{y_{std\_dev}}}$
WW	14.43	1
PW	17.47	1
YW	20.58	1
FLW	31.33	1

Note. Live weight data were divided into four age categories based on the age of the animal when it was weighed. The age categories were as follows: 181 days to 280 days (weaning weight, WW), 281 days to 380 days (puberty weight, PW), 381 days to 480 days (yearling weight, YW), 791 days to 940 days (first lactation weight, FLW).

9.5. Markov-chain Monte Carlo (MCMC) samples for each of the four univariate analyses

9.5.1. Weaning Weight (WW)

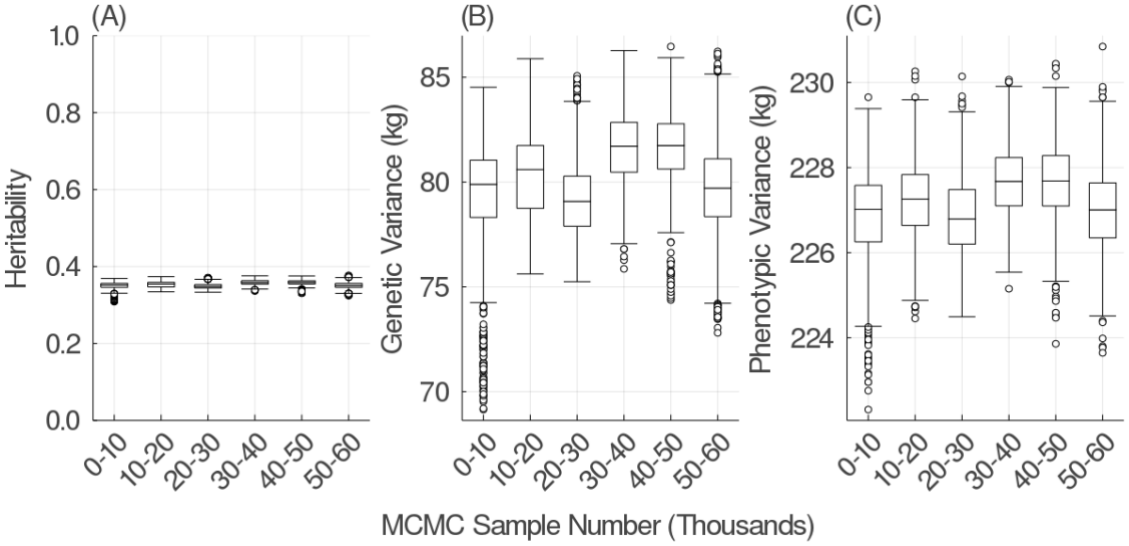

Figure 5 Posterior means of the Markov chain (bins of 10,000) for univariate analysis of weaning weight (age category: 181 days to 280 days). Weaning weight heritability (A), weaning weight genetic variance (B), weaning weight phenotypic variance (C). MCMC = Markov-chain Monte Carlo.

9.5.2. Puberty Weight (PW)

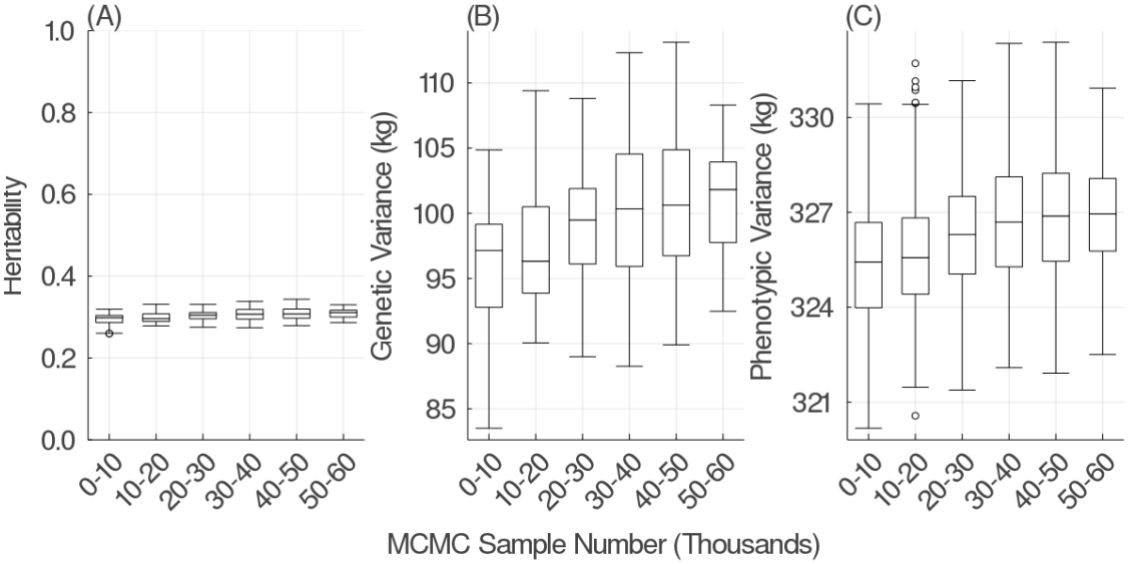

Figure 6 Posterior means of the Markov chain (bins of 10,000) for univariate analysis of puberty weight (age category: 281 days to 380 days). Puberty weight heritability (A), puberty weight genetic variance (B), puberty weight phenotypic variance (C). MCMC = Markov-chain Monte Carlo.

9.5.3. Yearling Weight (YW)

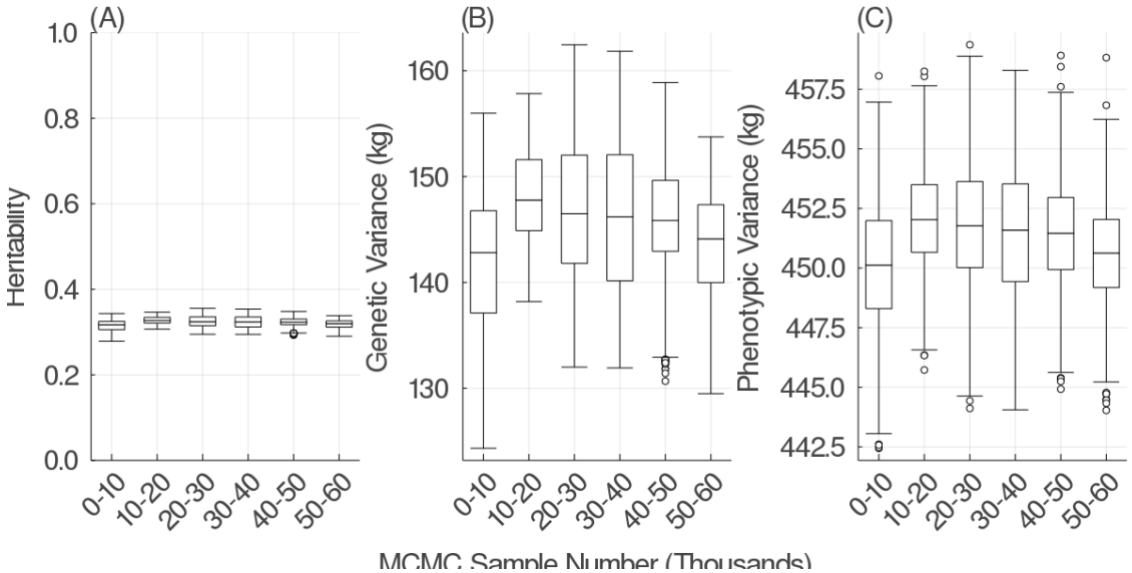

Figure 7 Posterior means of the Markov chain (bins of 10,000) for univariate analysis of yearling weight (age category: 381 days to 480 days).
Yearling weight heritability (A), yearling weight genetic variance (B), yearling weight phenotypic variance (C). MCMC = Markov-chain Monte Carlo.

9.5.4. First Lactation Weight (FLW)

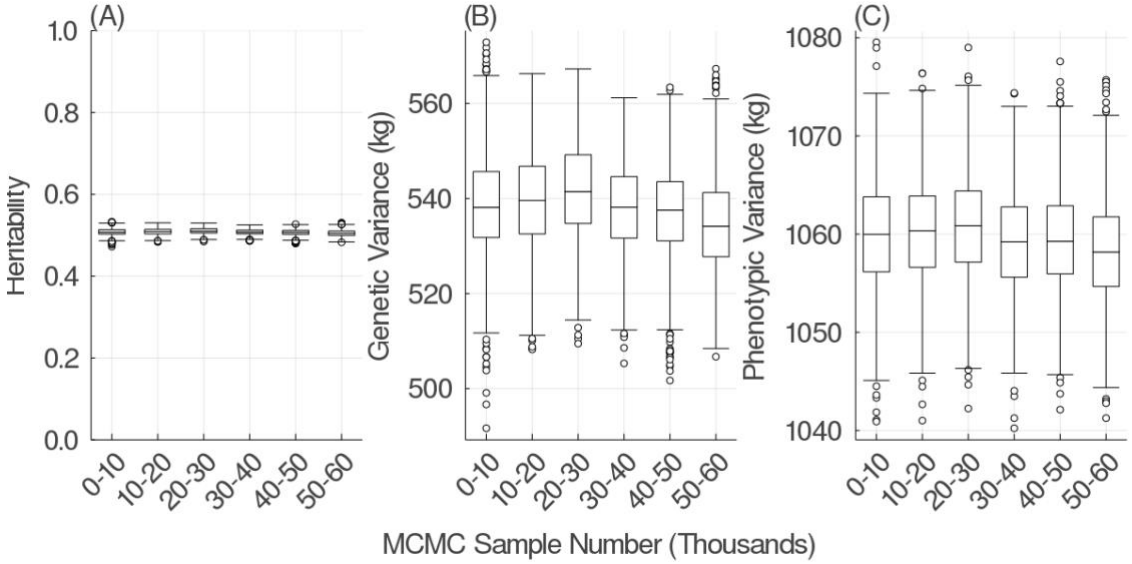

Figure 8 Posterior means of the Markov chain (bins of 10,000) for univariate analysis of first lactation weight (age category: 791 days to 940 days).
First lactation weight heritability (A), first lactation weight genetic variance (B), first lactation weight phenotypic variance (C). MCMC = Markov-chain Monte Carlo.

9.6. Markov-chain Monte Carlo (MCMC) samples for each of the six bivariate analyses

9.6.1. Weaning Weight (WW) with Puberty Weight (PW)

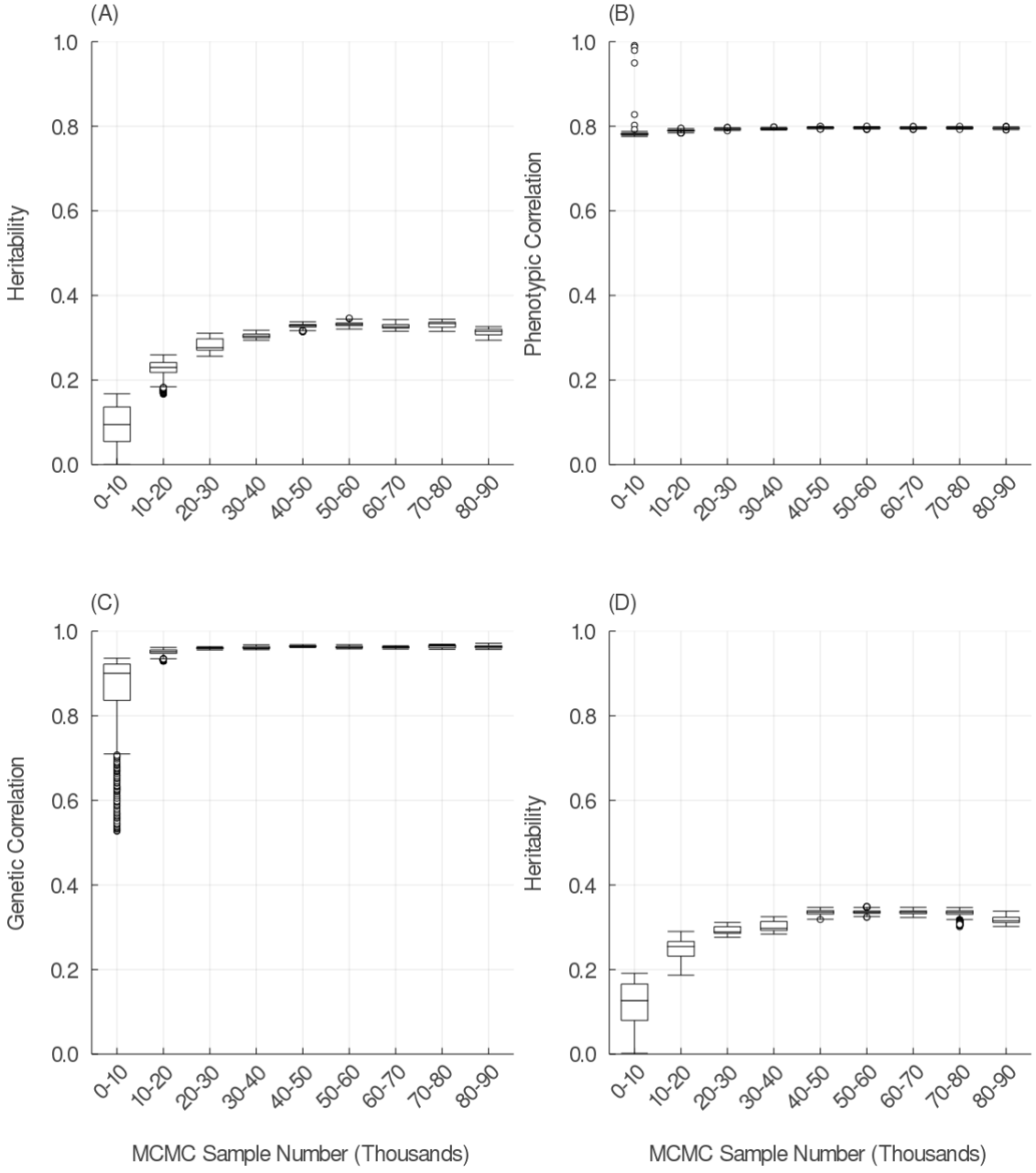

Figure 9 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of weaning weight and puberty weight.
Weaning weight heritability (A), phenotypic correlation (B), genetic correlation (C), puberty weight heritability (D). MCMC = Markov-chain Monte Carlo.

9.6.2. Weaning Weight (WW) with Yearling Weight (YW)

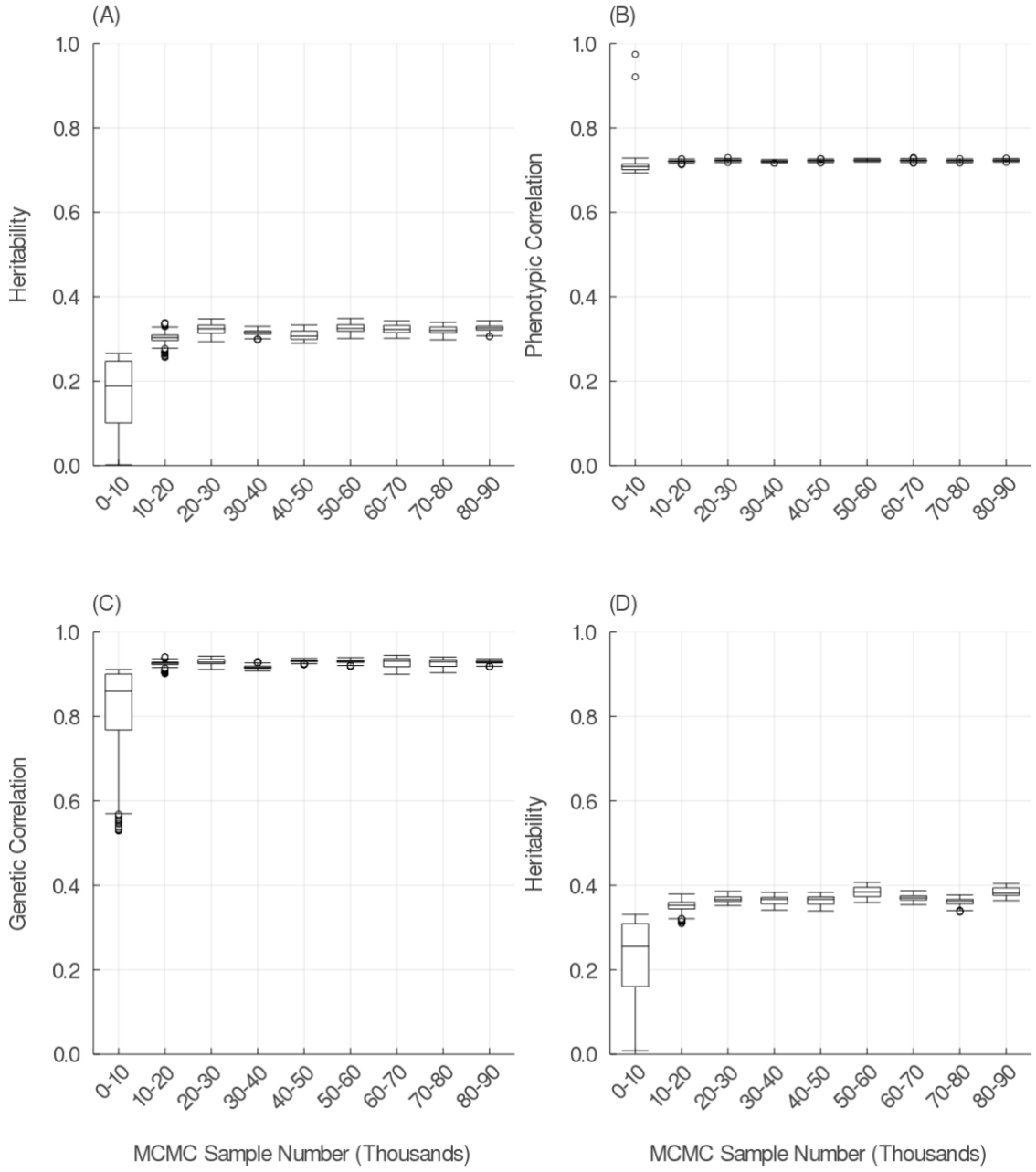

Figure 10 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of weaning weight and yearling weight.
Weaning weight heritability (A), phenotypic correlation (B), genetic correlation (C), yearling weight heritability (D).

9.6.3. Weaning Weight (WW) with First Lactation Weight (FLW)

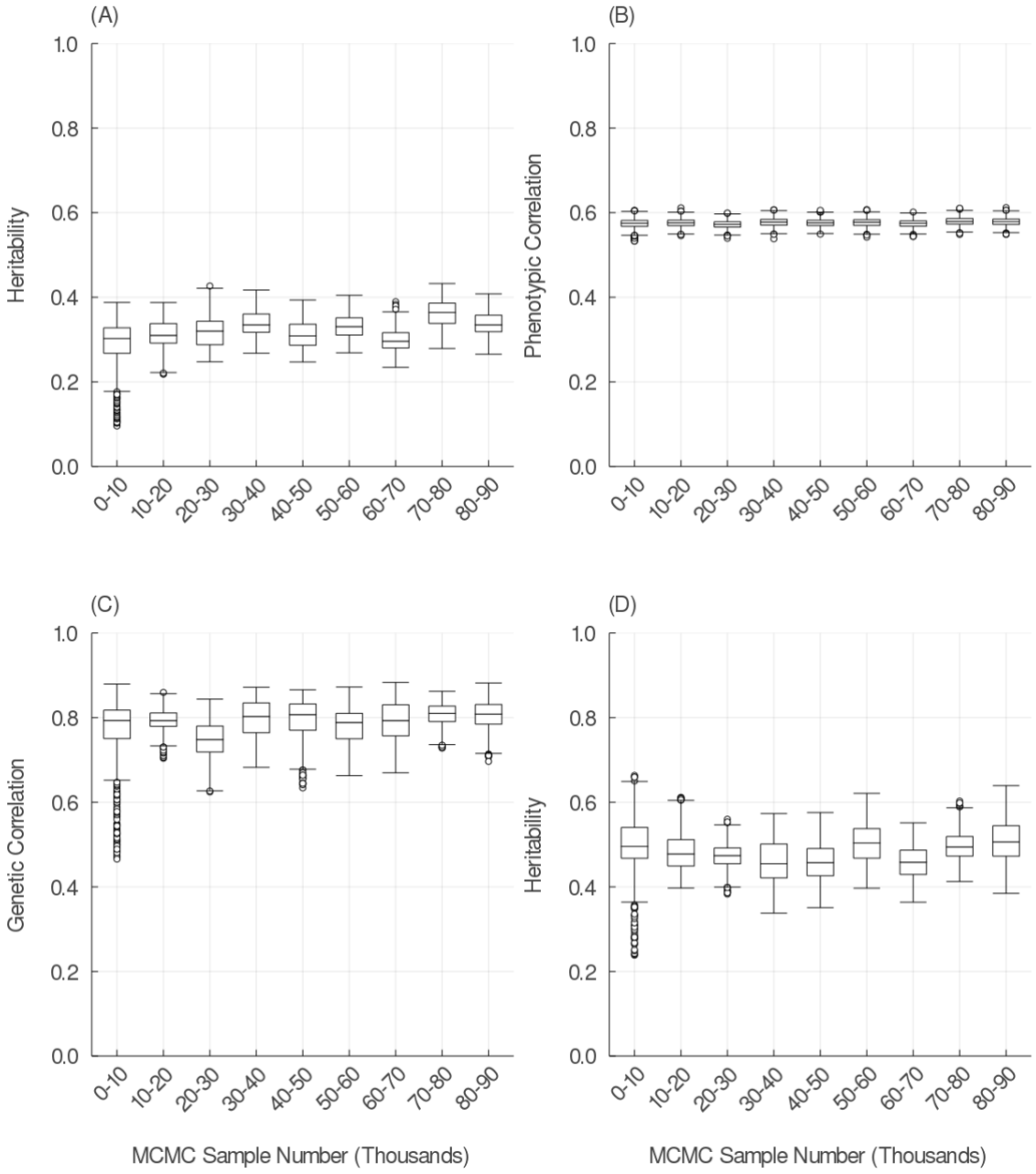

Figure 11 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of weaning weight and first lactation weight.
Weaning weight heritability (A), phenotypic correlation (B), genetic correlation (C), first lactation weight heritability (D).

9.6.4. Puberty Weight (PW) with Yearling Weight (YW)

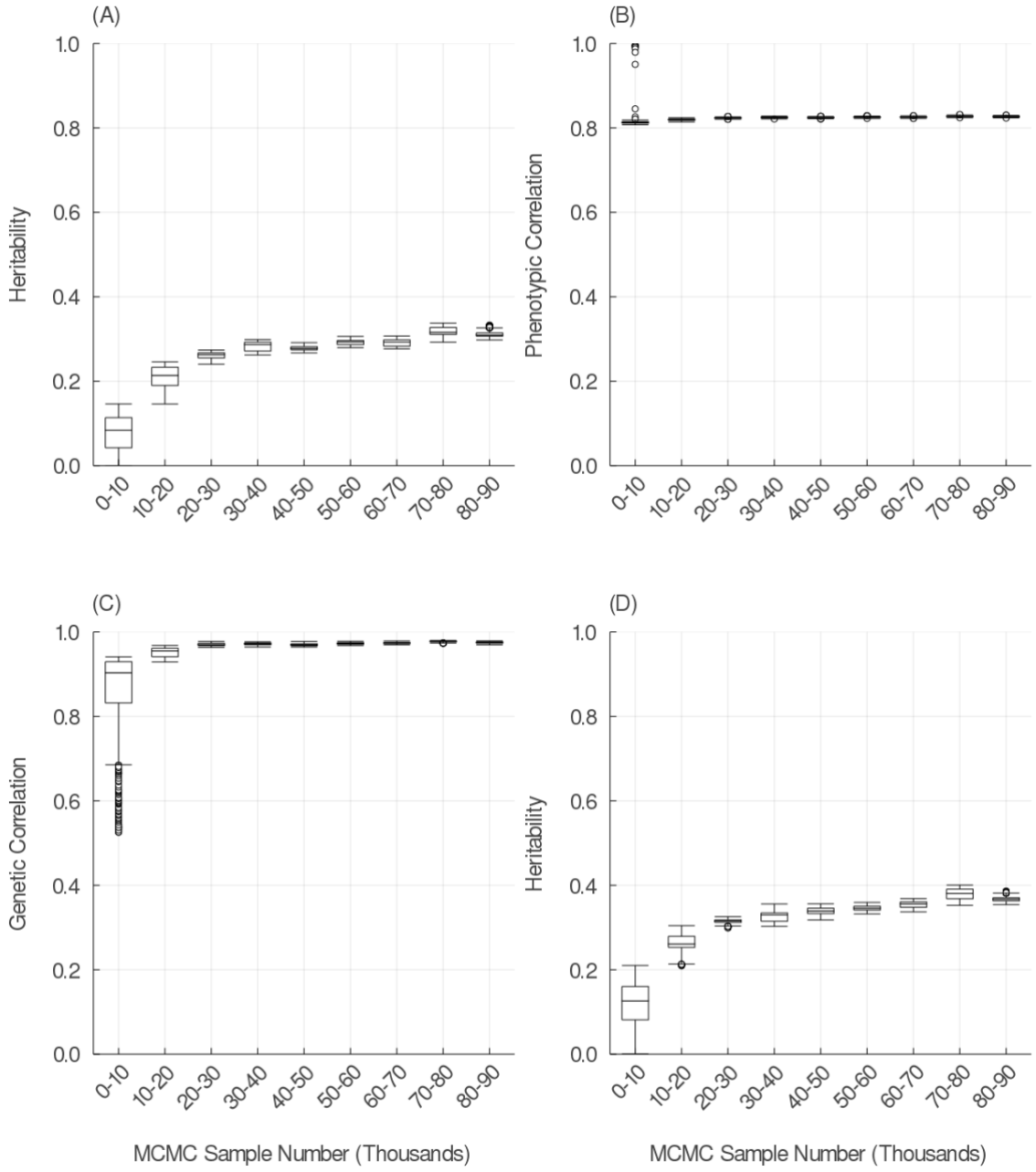

Figure 12 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of puberty weight and yearling weight.
Puberty weight heritability (A), phenotypic correlation (B), genetic correlation (C), yearling weight heritability (D).

9.6.5. Puberty Weight (PW) with First Lactation Weight (FLW)

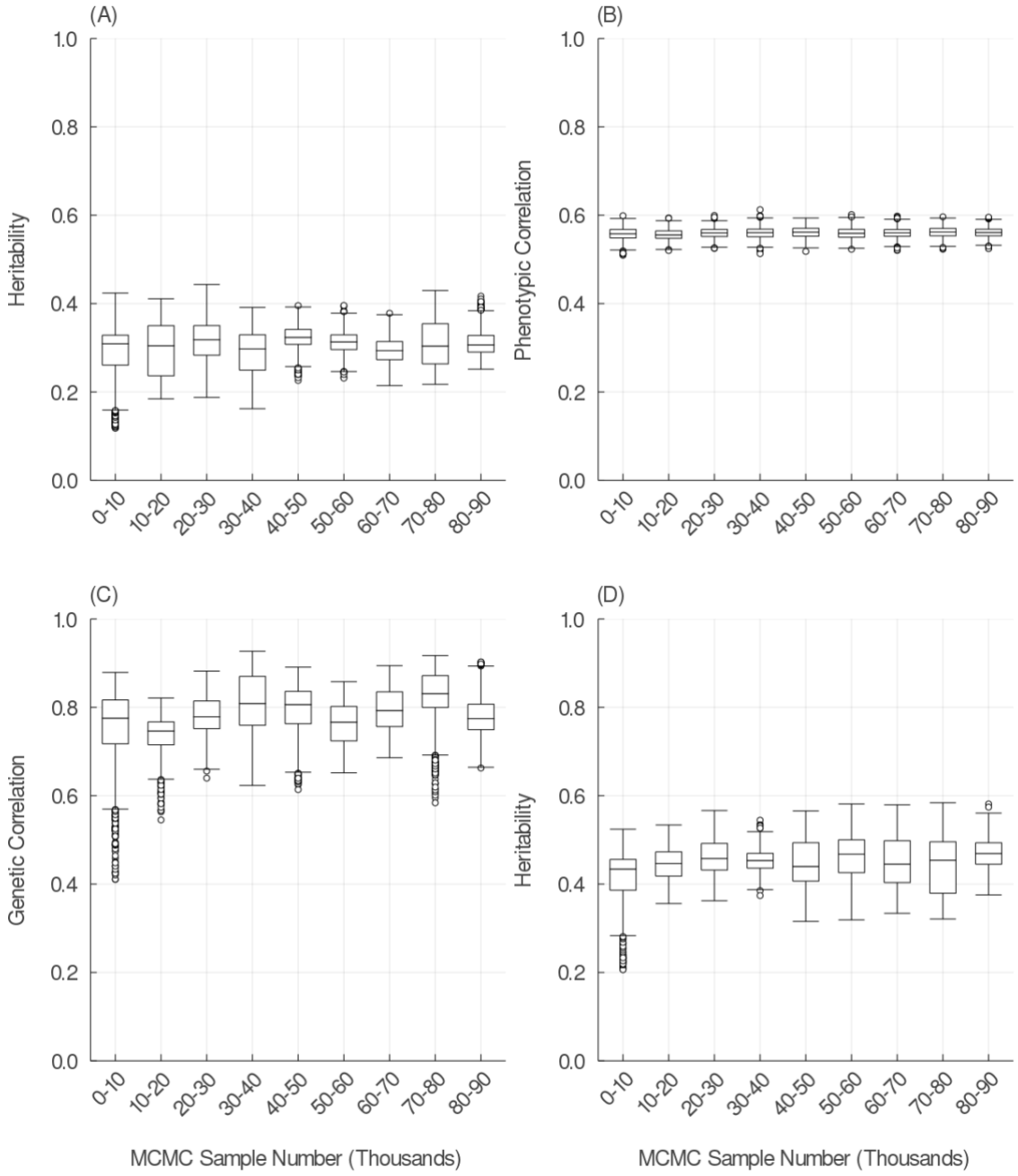

Figure 13 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of puberty weight and first lactation weight.
Puberty weight heritability (A), phenotypic correlation (B), genetic correlation (C), first lactation weight heritability (D).

9.6.6. Yearling Weight (YW) with First Lactation Weight (FLW)

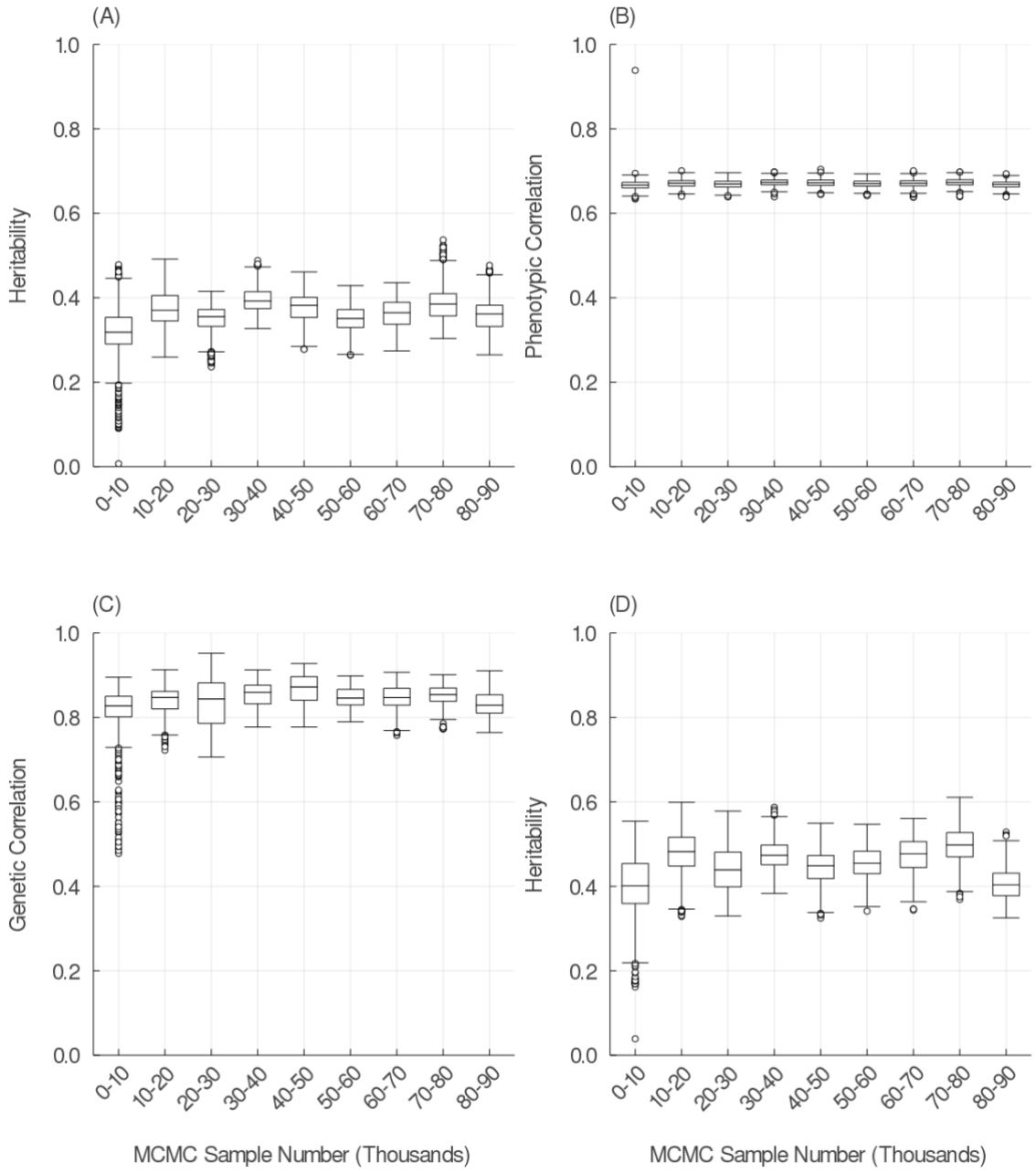

Figure 14 Posterior means of the Markov chain (bins of 10,000) for bivariate analysis of yearling weight and first lactation weight.
Yearling weight heritability (A), phenotypic correlation (B), genetic correlation (C), first lactation weight heritability (D).

9.7. Markov-chain Monte Carlo (MCMC) samples for Repeated Measures

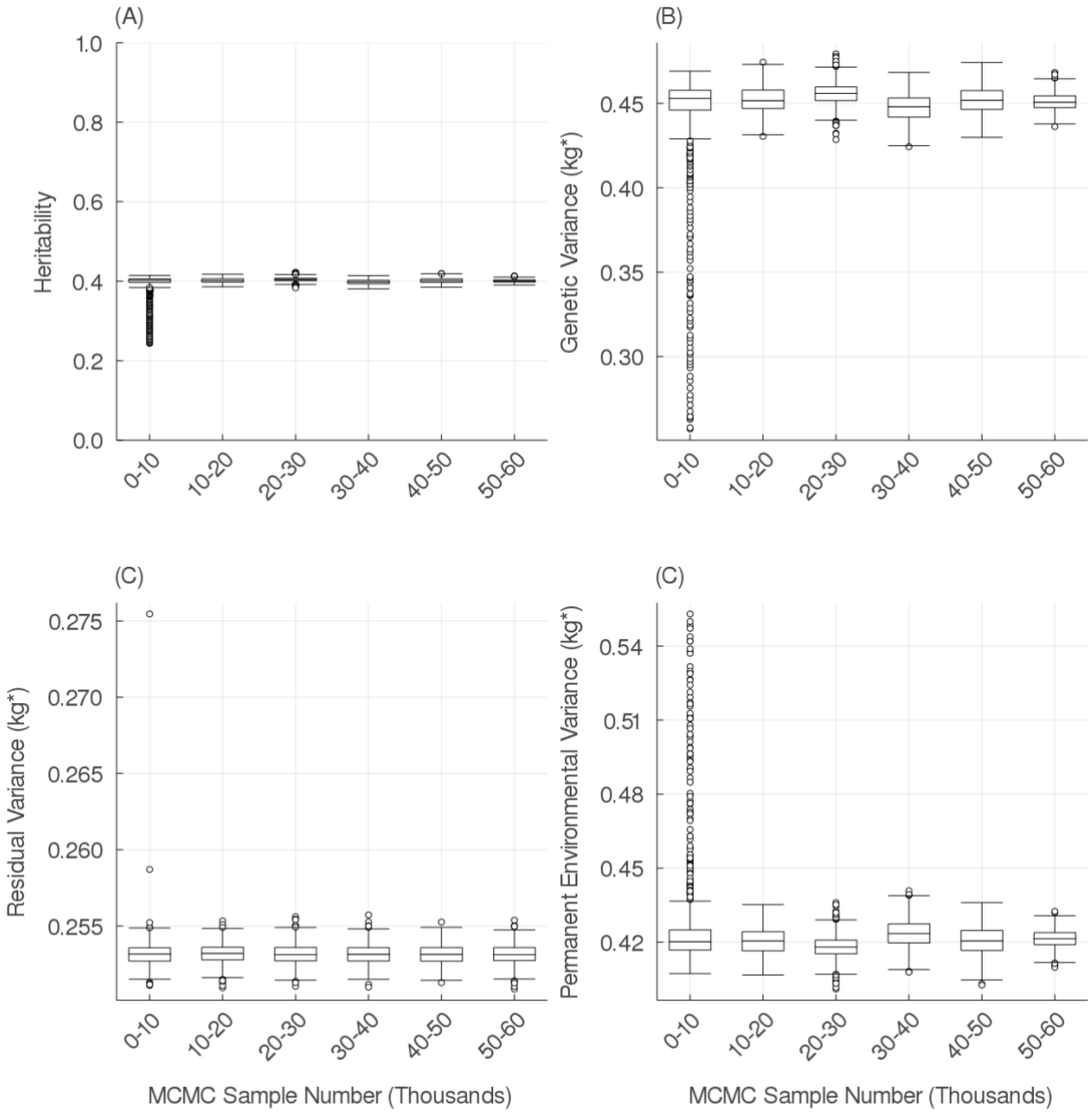

Figure 15 Posterior means of the Markov chain (bins of 10,000) for repeated measures analysis of live weights from four age categories.
Heritability (A), genetic variance (B), residual variance (C), Permanent environmental variance (D). Age categories included were weaning weight: 181 days to 280 days, puberty weight: 281 days to 380 days, yearling weight: 381 days to 480 days, first lactation weight: 791 days to 940 days. *Phenotypes included in this analysis were pre-adjusted for fixed effects and standardised for variance. Units were kg/mean variance of the relevant age category.

10. Model Validation Statistics

Four univariate analyses, and one repeated measures analysis were validated using standard validation techniques (Table 18).

Table 18 Model validation results for each of the four univariate analyses (WW, PW, YW and FLW) and the repeated measures analysis (All).

Statistic	WW	PW	YW	FLW	All
Number of animals	271,794	185,101	191,109	146,444	515,476
Number of validation animals	47,122	34,446	37,104	5,955	67,328
Mean Bias	0.09	-0.01	-0.10	0.21	-0.004
Change in dispersion	1.00	0.98	0.97	0.99	0.98
Population accuracy	0.70	0.74	0.74	0.53	0.65

WW (weaning weight): univariate analysis including live weights obtained when animals were 181 days to 280 days old. PW (puberty weight): univariate analysis including live weights obtained when animals were 281 days to 380 days old. YW (yearling weight): univariate analysis including live weights obtained when animals were 381 days to 480 days old. FLW (first lactation weight): univariate analysis including live weights obtained when animals were 791 days to 940 days old. All: repeated measures analysis included live weight phenotypes from WW, PW, YW and FLW age categories. For a full description of each validation technique see Section 5.3.6.

11. Bash Scripts

See below link for bash scripts

https://github.com/melissa-stephen/masters_thesis